POPULATION PROCESSES IN ESTUARINE LITTORAL NEMATODES

by

Michael Hodda

A thesis submitted for the degree of Master of Science
at the
Australian National University

November 1984

This thesis is my own work, apart from those sections where appropriate acknowledgement is made.

Michael Hodda

Michael E. Hodda

ACKNOWLEDGEMENTS

The work reported in this thesis was carried out from March 1983 to July 1984 during the tenure of an Australian National University Master Degree Scholarship in the Department of Zoology. I should like to express sincere gratitude to my supervisor, Dr W.L. Nicholas, for his interest, stimulating comments during the course of the work and criticism of the manuscript. I also wish to record my appreciation to all members of the Department of Zoology, who by individual assistance and collective support have provided an environment without which this work would have been impossible. In particular, I wish to thank Dr P.J. Gullan and Professor C. Bryant for helpful criticisms of the manuscript and Dr T.G. Marples for fruitful discussion on ecological theory.

I am grateful to Mr R.B. Cunningham (Dept of Statistics) for advice on statistical methods and Genstat programming; to Mr G.B. Barlow and Ms K. Handel (Computer Services Centre) for advice on the optimal use of the computing resources at ANU; and to the Operations Staff at the Computer Services Centre for their care in plotting the figures.

Finally, I wish to thank Mrs D. Kjeldsen for her endless patience in typing the numerous drafts of this thesis.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

SUMMARY

This thesis describes a study of the population processes operating in estuarine littoral nematodes in New South Wales on three widely different spatial scales over one year. Data from extensive surveys of nematodes in three estuaries were investigated using factor and cluster analyses to assess the relative importance of the differences in population characteristics between the different estuaries, between different sites within an estuary and between different samples at the same site. The importance of deterministic and stochastic processes in controlling population characteristics on each scale was also assessed according to whether there were any patterns in the populations which were related to environmental factors. The operation of these processes was further investigated in a simple laboratory system.

No single scale of change in population characteristics was overwhelmingly important, nor were the populations controlled predominantly by either deterministic processes. Rather, the total variation in population characteristics was partitioned as follows.

* About 35% was due to stochastic variation on the small scale within each site. Patterns of dispersion and dispersal in laboratory populations was consistent with this.
* About 50% of population variability was due to deterministic patterns among the sites on the medium scale. The most important patterns were caused by the grain size and redox potential of the sediment and the distribution of surface algae. These factors affected the relative abundance of three major groups of species. Both field and laboratory data indicated that these factors influence the density of at least some species directly, and not through interspecific competition.

* About 5% of population variability was due to large scale changes between the different estuaries but the nature of this change could not be ascertained.
* About 23% of population variability was due to changes over time. 8% of this was uniform change over all the sites and 15% was change which was different at each site (also included in the variation allocated to medium scale change). Whether the temporal change was repeatable seasonal change or otherwise could not be ascertained.

This allocation of variability in population characteristics has considerable implications for ecological theory, the biology of estuarine nematodes and future study on these animals, which are discussed. The utility of the statistical approaches used in this study is also discussed.

CHAPTER 1

INTRODUCTION

1.1 *INTRODUCTION*

Although not visually obvious, many very small metazoan animals live in marine and estuarine sediments. Collectively termed the meiofauna these animals will pass through a 2.0 mm mesh sieve yet include a bewildering array of different phyla and species. Members of the meiofauna may be small and obscure but there are such enormous numbers of them in every square metre of sediment that they are important to many ecosystems in recycling nutrients and providing significant links near the base of many food chains. Meiofaunal populations in estuaries are particularly important because of the many conflicting human uses of estuaries for waste disposal, industry, fisheries and recreation. Yet very little is known about the meiofauna generally and almost nothing of the meiofauna in Australia.

Nematodes dominate the meiofauna in number of individual animals and number of species. However only a limited number of studies have described estuarine littoral nematode populations and none have attempted a comprehensive coverage of the different agents affecting the nematode populations and how they operate. Thus, although the effects of various environmental components and interspecific competition have been separately emphasised, the relative effect of each on nematode populations is unknown and the effects of random variation and predation have been largely ignored. Changes in nematode populations over time and over different scales of space have also received scant attention. Hence this study examines three estuarine littoral nematode populations to determine the relative importance of different ecological agents and processes in controlling some of the characteristics of nematode populations in space and time, and the scales on which these processes operate.

1.2 *DEFINITION OF TERMS*

In community ecology, many different terms have been used to describe the same population characteristics and some terms have different meanings to different authors. As there is no standard nomenclature, the terminology used throughout this thesis is presented below.

Term	Usage
(species) composition	which species are present
(population) structure	statistical distribution of animals among species irrespective of species identities.
(species) density	density of one species
nematode density	density of all species
total density	density of all species
population parameters	all the above
population characteristics	all the above
relative abundance	proportion of total population of one species.
assemblage	any group of species occuring together
population	any group of species occuring together
distribution	spatial pattern of occurrence

1.3 *ECOLOGICAL THEORY*

Two general mechanisms are capable of regulating the organisation of biotic communities. Termed deterministic and stochastic processes (*sensu* Grossman 1982 and Sale 1977), they operate very differently and have wide implications for the biology of the organisms involved (Connell 1978; Sale 1977, 1979, 1980; Sousa 1979a).

When species assemblages are regulated by deterministic processes, the presence and relative abundance of species is determined by the biotic and/or abiotic environment. Consequently, where biotic succession occurs the population parameters of the assemblage at any time are predictable from a knowledge of the species composition and

population structure at the preceding time. Alternatively, the population characteristics may be predictable from a knowledge of the precise conditions at, and history of, an area.

In communities regulated by deterministic processes the pattern of occurrence of any species may be maintained in four ways. First, coexisting species may partition a single limiting resource and regulate density through interspecific competition (Schoener 1974b). Second, the occurrences of a species may be limited by physiologically unfavourable environmental conditions (Terbourgh 1971). Third, many species may intercompete for different resources so that each species is competitively dominant for some resources but inferior for others (Buss and Jackson 1979; Kastendiek 1982). Fourth, selective predation may regulate the pattern of occurrence of certain species and facilitate the coexistence of competitive inferiors which would otherwise be excluded by competition (Connell 1975; Glasser 1979; Harper 1969; Paine 1966; Roughgarden 1974; Roughgarden and Feldman 1975). Despite some minor criticism (eg Abrams 1977), deterministic processes have been widely recognised for a long time as capable of regulating animal populations, although under different names (Lotka 1932; Nicholson 1933, 1954; Volterra 1926).

Recognition that stochastic processes may operate in animal populations is more recent (Andrewartha and Birch 1954). In species assemblages regulated by stochastic processes, where a species occurs, and which species occur together are not predictable because random variations in resource availability and/or physical disturbance of the environment continually change the distribution of species (Andrewartha and Birch 1954; Chesson and Warner 1981; Connell 1975; Horn and MacArthur 1972; Levins and Culver 1971; Lewontin 1969; Slatkin 1974). Hence the population characteristics at any place or time cannot be predicted *a priori* (Connell 1978; Grossman 1982; Levin 1974; Levin and

Paine 1976; Sale 1975, 1979; Sousa 1979a). Biological interactions are not important and two species may be perfect competitors without one competively excluding the other (Huston 1979; Sale 1975, 1977).

Many studies have cited the exclusive operation of either deterministic or stochastic processes. However, there appears no general association of either process with the type of animals being considered, their sizes or the environments in which they are found. The influence of stochastic processes has been emphasised by many authors in the control of various population parameters. Many small organisms and marine animals are involved (Table 1.1). However, deterministic processes have been emphasised for other small organisms and other marine assemblages (Table 1.2). Even though deterministic processes are almost always cited in terrestrial vertebrates (Brown and Lieberman 1973; Cody 1968; Diamond 1975; Jaeger 1971; Pianka 1976; Pulliam 1975; Schoener 1974a), there are still exceptions (Connor and Simberloff 1979). All four theoretical mechanisms of deterministic processes have been observed in field populations. The various forms of interspecific competition are emphasised most often but predation and the environment sometimes have important effects (Table 1.3). Different mechanisms determine the population structure of very similar organisms in some cases but in many cases all three mechanisms are involved (Table 1.3).

Which of these two processes controls the structure of a particular population may be related to the rate of unpredictable changes in the environment (Grossman 1982; Huston 1979; Osman 1977; Sousa 1979a; Yodzis 1982). Others disagree (Eagle 1975; Sanders 1968) and a few workers doubt the existence of any unifying pattern (Eagle and Hardiman 1977). However, each process has been implicated exclusively in coral reef fish; stochastic processes by Sale (1977), Sale and Dybdahl (1975) and Talbot, Russell and Anderson (1978); deterministic processes by Anderson, Ehlich, Ehlich, Roughgarden, Russell and Talbot (1981) and Roughgarden (1974). Observations on other assemblages, however suggest

TABLE 1.1 Organisms on which Stochastic Processes Operate

Organisms	Reference(s)
Diatoms	Patrick 1967
Protozoa	Cairns, Plafkin, Kaesler and Lowe 1983; Cairns, Ruthven and Kaesler 1972; Dickson and Cairns 1972; Kaesler and Cairns 1969, 1972.
Small Metazoa	Dickson and Cairns 1972
Fouling Organisms	Fager 1977
Sessile Hard-substrate Macrofauna	Dayton 1971, 1973; Sousa 1979b; Woodin 1978;
Soft-substrate Macrofauna	Boesch, Wass and Virnstein 1976; Davis and Van Blaricom 1978; Keough 1983; Osman 1977; Sutherland and Karlson 1977
Sub-littoral Epiphytes	Fletcher and Day 1983
Sand-bar Copepods	Hockin and Ollason 1981
Epizoic organisms on Corals	Jackson 1977

TABLE 1.2 Organisms on which Deterministic Processes Operate

Organisms	Reference(s)
Tide Pool Fish	Grossman 1982
Coral Reef Molluscs	Kohn 1959, 1968, 1971
Hard-substrate Macrofauna	Lubchenko 1980; Menge 1976
Soft-substrate Macrofauna	Kent 1983; Rex 1977
Amphipods	Fenchel and Kolding 1979; Van Dolah 1978

TABLE 1.3 Reports of Deterministic Mechanisms

Mechanism	Organism(s)	Reference
Interspecific Competition	Cave communities	Culver 1970
	Birds	Karr 1971; Orians and Horn 1969
	Benthic macrofauna	Kastendiek 1982; Peterson 1975; Rainer 1981; Rex 1977; Van Blaricom 1982; Woodin 1974
	Corals	Lang 1973; Porter 1972b
	Lizards	Pianka 1967, 1969, 1971; Schoener 1968
	Crabs	Vance 1972
Predation	Forest trees	Janzen 1970
	Benthic macrofauna	Levinton and Stewart 1982; Virnstein 1977
	Rocky intertidal communities	Paine 1971
	Corals	Porter 1972a
Environment	Amphipods	Kneib 1982
	Crabs	Taylor 1982
All the above	Amphipods	Fenchel and Kolding 1979; Van Dolah 1978
	Corals	Day 1977; Porter 1974
	Marine gastropods	Kent 1983
	Encrusting organisms	Jackson and Winston 1982
	Intertidal algae	Lubchenko 1980
	Rock intertidal community	Menge 1976; Paine 1966
	Salt marsh macrofauna	Vince, Valiela, Backus and Teal 1976

a solution to this conflict: both deterministic and stochastic processes operate on many populations to varying degrees (Table 1.4). Hence the relative importance of each process remains a pressing question in community ecology (Connell 1978; Grossman 1982; Sousa 1979a).

Many of the studies with conflicting results, however, consider different population sizes and areas. The different scales studies may account for some of the conflict (Anderson *et al.* 1981), but the influence of scale remains largely ignored.

1.4 *ECOLOGY OF ESTUARINE NEMATODES*

Meiofauna generally and nematodes in particular are ideal organisms on which to study the mechanisms of community organisation. Nematodes generally reproduce relatively rapidly and live in diverse assemblages within a complex multi-level environmental mosaic. These features make estuarine littoral nematode populations a microcosm of much larger and more complex communities which function over much larger areas and longer times. However, the specialised skills required for observation and manipulation, and the proportionally greater time required for identification of such small organisms has limited both the number and range of ecological studies on nematodes. So, although neither deterministic nor stochastic processes have been directly investigated in nematodes, many isolated and independent observations suggest the operation of one process or the other. Many different marine nematode communities are considered in the following review because there is very little information available on estuarine littoral nematodes.

TABLE 1.4 Observations of both Deterministic and Stochastic Processes

Organisms	References
Barnacles	Connell 1961, 1970
Coral Reef Communities	Connell 1978
Corals	Glyn 1976; Loya 1976
Polychaetes	Dauer & Simon 1976
Molluscs	Jackson 1972
Rocky Intertidal Communities	Lubchenko & Menge 1978; Osman 1977
Encrusting Organisms on Boulders	Sousa 1979a, b

1.4.1 Deterministic Processes

a) *Environment*

Many components of the environment influence various nematode populations but they often work by different mechanisms and operate on different scales of space and time. Different components seem to influence different population parameters and some affect only certain nematode species; the effects of others are inconclusive or contradictory.

Much controversy surrounds the effect of pollution on nematode populations (Coull, Hicks and Wells 1981; Raffaelli 1981; Raffaelli and Mason 1981; Warwick 1981b). Pollutants have been claimed to increase nematode density (McLachlan, Winter and Botha 1977; Van Es, Van Arkel, Bouwman and Schroder 1980; Wormald and Stirling 1979), decrease density (Amjad and Gray 1983; Coull and Wells 1981; Read, Anderson, Matthews, Watson, Halliday and Sheils 1983; Rutzler and Sterrer 1970; Wormald 1976) and have no effect on nematode density (Boucher 1980; Gray 1971; Marcott and Coull 1974; Tietjen 1980b; Vidacovic 1983). Claims that pollution affects species composition and diversity by some (Giere 1979; Gray 1981; Heip and Decraemer 1974; Shaw, Lambshead and Platt 1983; Tietjen 1980b) are disputed by others (Tietjen 1977). Although some pollutants may directly affect nematode physiology (Howell 1983), all these conflicting observations may also be explained by changes in other components of the environment caused by pollution, for example nutrient availability (Wormald 1976) or redox potential (Giere 1979) (see below).

Temperature may influence nematode distribution by affecting population growth rate and generation time (Gerlach and Schrage 1971; Heip, Smol and Absillis 1978; Hopper, Fell and Cephalu 1973; Tietjen and Lee 1972; Tietjen, Lee, Rullman, Greengart and Trompeter 1970; Warwick 1981a), reproductive potential (Heip *et al.* 1978; Hopper and Meyers 1966; Tietjen and Lee 1972, 1977a; Tietjen *et al.* 1970; Warwick 1981a) and metabolic rate (Price and Warwick 1980; Wieser and Schiemer 1977).

However, it is probably only of importance to the distribution of estuarine littoral nematodes on a global scale or during periods of drought or exceptional temperature extremes (Tietjen and Lee 1977a).

On a smaller scale, within single estuaries salinity has been implicated in controlling nematode distributions (Capstick 1959; Warwick 1971) and density (Van Es *et al.* 1980) but the only experimentally demonstrated effect on nematode populations is one similar to that of temperature on reproduction and growth (Tietjen and Lee 1972, 1977a; Tietjen *et al.* 1970; Warwick 1981a). However only some species are affected (Ott and Schiemer 1973) and mortality only occurs at very extreme salinities (Tietjen and Lee 1977a). Also many other environmental factors change concurrently with salinity as one heads inland from a river mouth. Among these factors are microbial populations (Ubben and Hansen 1980) and the grain size distribution of the sediment.

Indeed, grain size characteristics are very frequently and independently associated with nematode density (Maguire 1977), diversity (Heip and Decraemer 1974; Hopper and Meyers 1967a; Wieser 1960) and species distributions (Glemarec and Menesguen 1980; Tietjen 1977; Vitiello 1970; Ward 1973, 1975; Warwick 1971; Warwick and Buchanan 1970; Willems, Vincx, Claeys, Vanosmael and Heip 1982; Wieser 1960) but any such relationship is apparently not universal (Vidacovic 1983). Grain size may affect nematodes directly by the space available between sediment particles (Aller and Yingst 1978; Nicholas 1984; Tietjen 1977; Wieser 1960) or indirectly by some other factor related to grain size such as moisture content (Jansson 1967; Rees 1940), hydrodynamic regime (Rees 1940) or amount or type of food available (Van Es *et al.* 1980; Ward 1975). Among these, water movement (Boaden 1968), water content (Glemarec and Menesguen 1980; Warwick 1971) and detrital quality (Warwick 1971) have all been independently associated with nematode distributions.

The amount of oxygen available in a sediment may also be associated with grain size and it too may affect the distribution of nematode species. However, changes in vertical profiles of total nematode density have been emphasised rather than horizontal changes (Aller and Yingst 1978; Boaden 1977; Ott and Schiemer 1973; Sikora and Sikora 1982). The vertical distribution of some species is also affected (Fenchel and Reidl 1970; Kemp, Wetzel, Boynton, D'Elia and Stevenson 1981; Maguire 1977; Ott and Schiemer 1973; Teal and Wieser 1966; Tietjen 1969; Wieser and Schiemer 1977; Wieser, Ott, Schiemer and Gnaiger 1974). Some nematode migrations may be related to oxygen potential (Boaden and Platt 1971; Rieger and Ott 1971) although oxygen availability may have no effect on certain species that can live without oxygen for considerable periods (Boaden 1977; Teal and Wieser 1966). Nevertheless, oxygen availability may affect the horizontal distribution of nematodes either directly (Chandler and Fleeger 1983; Glemarec and Menesguen 1980) or through its association with tracheophyte root density (Osenga and Coull 1983). Lack of oxygen may also affect nematode density by affecting the hatching of nematode eggs or by causing defaunation of areas of anoxic mud (Coull 1969; Sherman and Coull 1980). However, there are many other chemical reactions within littoral sediments which are related to oxygen levels (McLachlan 1978; Patrick and DeLaune 1977) and furthermore oxygen levels are influenced by other factors as well, such as macrofaunal burrows (Aller and Yingst 1978), which superimprose an ephemeral small scale mosaic over any permanent large scale pattern in oxygen levels.

Many environmental factors may influence nematode populations over small areas and brief intervals. Meiofaunal nematodes are preyed on by a variety of macrofaunal invertebrates (Bell 1980; Bell and Coull 1978; Bilio 1967; Coull 1973; Platt 1981; Platt and Warwick 1980) and juvenile fish (Cain and Dean 1975; Fleeger 1980; Lassere, Renaud-Mornant and Castel 1976; Odum 1970). However in the absence of any direct evidence it is uncertain whether nematodes form a major part of macrofaunal diets (Platt and Warwick 1980) or only a small part of the

diet (Gerlach and Schrage 1969; Hylleberg 1975; McIntyre 1969; Platt and Warwick 1980; Reise 1979; Warwick and Price 1975). Macrofaunal predation may sometimes regulate total nematode density (Bell 1980; Bell and Coull 1978; McIntyre 1968) and distribution (Rees 1940), but this is not always observed (Fleeger, Whipple and Cook 1982) since meiofaunal nematodes may also compete with juvenile macrofauna for food (Fauchauld and Jumars 1979; Fenchel 1970; McIntyre 1964; McIntyre and Murison 1973; Thorson 1966 but *cf* Gerlach 1978 for a counter opinion). Macrofaunal tubes and burrows also affect nematode density (Findlay 1981; Lee, Tietjen, Mastropaolo and Rubin 1977; Reise 1983; Teal and Wieser 1966) and distribution (Aller and Yingst 1978; Bell, Watzin and Coull 1978; Eckman 1979; Findlay 1981). However, their effect on nematode density is localised and ephemeral, and the real causes are microbial food organisms (Aller and Yingst 1978; Teal and Wieser 1966) and oxygen potentials (see above).

Food itself may directly affect the distribution of nematodes in three ways. First, different food types can support different population densities of certain species and can also affect reproduction (Findlay 1982). Second, some nematode species will only feed on certain foods (Gerlach 1978; Heip and Decaemer 1974; Lee *et al*. 1977; Tietjen and Lee 1977b). Other species are less selective and feed on a wider range of foods, but all are still fairly restricted in diet by buccal morphology (Alongi and Tietjen 1980; Boaden 1964; Boucher 1973; Deutch 1978; Tietjen and Lee 1977b; Wieser 1952, 1959, 1960). Third, nematodes may migrate toward certain food sources such as fungi (Hopper and Meyers 1966, 1967b; Meyers and Hopper 1973; Meyers, Hopper and Cefalu 1970), decaying fish (Gerlach 1977b), decomposing macrophytes (Hopper and Meyers 1967a; Koop, Newell and Lucas 1981) and mangrove leaves (Odum and Heald 1972). As expected from these observations, food is an important influence on the distribution of many individual nematode species (Findlay 1981; Hogue and Miller 1981; Warwick 1977). Total nematode density is also influenced by a number of features associated with the

amount of food in the sediment; carbon input (Chamroux, Boucher and Bodin 1979; Montagna and Ruber 1980; Wormald and Stirling 1979), carbon content (Glemarec and Menesguen 1980; Teal and Wieser 1966; Warwick 1971), nitrogen content (McLachlan *et al.* 1977), density of overlying tracheophyte vegetation and chlorophyll A distribution (Fleeger *et al.* 1982). Despite these observations the power of food in controlling the characteristics of the total population is not known (Lee *et al.* 1977). However, it is likely that food distribution has an important influence because many potential food organisms and substrates are distributed in strongly ephemeral patches (for example, mangrove leaves (Albright 1976; Odum and Heald 1975) and their associated micro-organisms (Cundell, Brown, Stanford and Mitchell 1979), epipelic algae (Baillie and Welsh 1980), bacteria (Fehon and Oliver 1979; Rublee 1981) and free amino acids (Gardner and Hansen 1979)).

b) *Competition*

Nematodes are relatively simple animals, limited in their possibilities to specialise on particular types of food by musculo-skeletal constraints. Hence many authors suspect interspecific competition to be important in nematode ecology because many species are thought to have overlapping food ranges. Both Wieser (1960) and Hopper and Meyers (1967a) inferred that competitive exclusion resulted in fewer nematode species occurring in homogeneous environments than in heterogeneous environments. However, competition may be more important among certain ecological groups of nematodes than others. For example, nematodes which suck fine food particles from suspension (deposit feeders) are less selective when feeding than those nematodes feeding by different means (Tietjen and Lee 1977b) and hence Tietjen (1977) inferred that intense competition for food particles of certain sizes amongst deposit feeders causes the numerical dominance of only a few species and low diversity which is typical of shallow marine muds (Boucher 1973; Heip and Decraemer 1974; Juario 1975; Tietjen 1976, 1977, 1980b; Warwick 1971; Warwick and Buchanan 1970; Wieser 1960). Similarly, lack of competition has been

invoked to explain nematode communities with low dominance and high diversity in mixed sediments (where food is more heterogeneous (Alongi and Tietjen 1980) and in the deep sea (where food is so scarce that nematodes must be so highly specialised to feed (Alongi and Tietjen 1980; Tietjen 1977)). Experimentally, competition between two species of deposit feeding nematodes decreased the population growth of both when together in laboratory populations compared with monospecific populations (Alongi and Tietjen 1980). Significantly, however, an algal feeding nematode did not compete with either of the deposit feeders, indicating that other factors are also likely to be important in controlling nematode population parameters in the laboratory. The relevance of these experiments to the field situation is uncertain.

c) *Predation*

Very little is known about predation on meiofaunal nematodes, but the available evidence suggests that selective predation is not likely to be particularly important in controlling the characteristics of nematode populations. Although many macrofauna and some fish may ingest nematodes, they are unlikely to select any particular species (Platt and Warwick 1980). Predators nearer in size to their nematode prey, such as small decapod and copepod crustacea (Platt and Warwick 1980), immature stages of annelids (Perkins 1958), turbellarians (Bilio 1967), hydroids (Heip and Smol 1976) and predaceous nematodes (Nicholas 1984), may feed more selectively, but almost nothing definitive is known of these interactions.

1.4.2 Stochastic Processes

Stochastic processes have not been directly demonstrated to act on estuarine nematode populations. However, some of the features associated with populations controlled by stochastic processes have been observed in estuarine nematode populations and their environments.

The sedimentary environment of nematodes is very patchy and fluctuates considerably (Boesch, Wass and Virnstein 1976; Buchanan, Kingston and Sheader 1974; Coull and Fleeger 1977; Davis and Van Blaricom 1978; Dugan and Livingston 1982; Dyer 1981; Eagle and Hardiman 1977; Goulter and Allaway 1979; Lewis and Platt 1981; Moll and Rohlf 1981; Peterson 1975; Rublee 1981; Warwick 1981a; Woodroffe 1981). Hence, it is not surprising that dispersal has often been thought significant in nematode ecology (Boaden 1964, 1968; Chandler and Fleeger 1983; Gerlach 1977a; Hagerman and Rieger 1981; Jensen 1981; Rieger and Ott 1971; Sherman and Coull 1980; Sibert 1981; Sterrer 1973; Surey-Gent 1981). However, although some studies have found rapid and extensive dispersal (Giere 1979; Hagerman and Rieger 1981), others find dispersal slow and effective over only short distances (Chandler and Fleeger 1983; Sherman and Coull 1980) and some authors consider that extensive dispersal occurs only during abnormal storms (Gerlach 1977a). Opinion also differs as to whether the colonising ability of nematodes is generally good (Bell 1979; Gerlach 1971; Hagerman and Rieger 1981; Warwick 1981b) or poor (Sterrer 1973; Swedmark 1964; Wieser and Kanwisher 1961). However some species have certainly been transported out of their normal intertidal habitats (Hagerman and Rieger 1981; Gerlach 1953) and species previously unknown or from quite different habitats have colonised defaunated sediment (Giere 1979) and artificial substrates (Lee *et al.* 1977). Population structure also changed substantially over time in a controlled experimental ecosystem (Chamroux *et al.* 1977a) and unpredictable and unexplainable yet very substantial changes in density occur frequently in field populations (Bell and Coull 1978; Hagerman and Rieger 1981; Lee *et al.* 1977; Reise 1983; Yingst 1978). All these observations indicate some unpredictability in estuarine nematode populations which is typically associated with stochastic processes. However, many other nematode populations have the very stable and predictable species compositions characteristic of communities controlled by deterministic processes (Boucher and Chamroux 1976; Capstick 1959; Juario 1975; Warwick 1971; Warwick and Buchanan 1971; Warwick and Price 1979).

1.5 *STUDY OBJECTIVES*

This study aims to investigate the relative importance of the different general ecological processes and the scales on which they operate in estuarine littoral nematode populations. To do this a number of distinguishing characteristics of field and laboratory populations were investigated. Data from a very extensive field survey was statistically examined to clarify the operation of the ecological processes in actual field populations. Manipulations of laboratory populations were used to verify the actions of these processes and examine the exact method by which the populations were affected.

Specifically this study examines:

(i) the relative amounts of random variation (generated by stochastic processes) and deterministic pattern (generated by deterministic processes) in species composition and abundance in the field;

(ii) the scale on which these processes operate by investigating the spatial distribution of stochastic variation and deterministic pattern;

(iii) the cause of any deterministic pattern by investigating the number of distinct nematode communities and their distribution in space and time;

(iv) by what mechanism the causes generate a deterministic pattern, by using patterns of species coexistence and distribution across environmental boundaries in both laboratory and field populations;

(v) whether the dispersal pattern of nematodes is suitable for the operation of stochastic processes.

Chapter 2 covers the general methods of these specific tasks while Chapter 3 deals generally with the relative importance of the different ecological processes and the scales of population change. Chapters 4 and 5 consider small scale changes and larger scale changes in more detail. Finally, Chapter 6 is a synthesis of all results and discussion of their broader ecological and nematological context.

CHAPTER 2

MATERIAL AND METHODS

2.1 *SAMPLING DATA*

2.1.1 Study Area and Scales of Sampling

Field data on the characteristics of nematode populations from estuarine littoral muds were statistically analysed over three different scales of sampling (Figure 2.1). The largest scale involved sampling at three hydrologically separate estuaries, at the Clyde River and Candlagan Creek on the NSW south coast, and at the Hunter River further north. The intermediate scale involved sampling at seven different areas (hereafter termed 'sites') scattered around a single estuary, the Hunter. The smallest scale involved small replicate samples ('replicates') taken only 1 cm from each other. These replicate samples were the basic unit of sampling: five replicates were taken at each of the seven sites in the Hunter estuary and at single sites in the Clyde and Candlagan estuaries. The range of scales covered is considerable; from about 300 km between the estuaries, to about 30 - 3000 m between the sites within a single estuary, and only about 1 cm between replicate samples within a single site. This is a range of seven orders of magnitude.

Table 2.1 shows the environmental characteristics of all the sites in the Hunter estuary and the single sites in the Clyde and Candlagan estuaries. However, no comprehensive tabulation of the micro-environmental characteristics of the small replicate samples is attempted because there are so many replicate samples and such a large variety of environmental components which may be of importance. These include the presence or absence of mangrove roots, pneumatophores, fallen leaves, pools of surface water or algal mats and all the other factors mentioned earlier (section 1.3).

FIGURE 2.1 STUDY AREA & SCALES OF SAMPLING

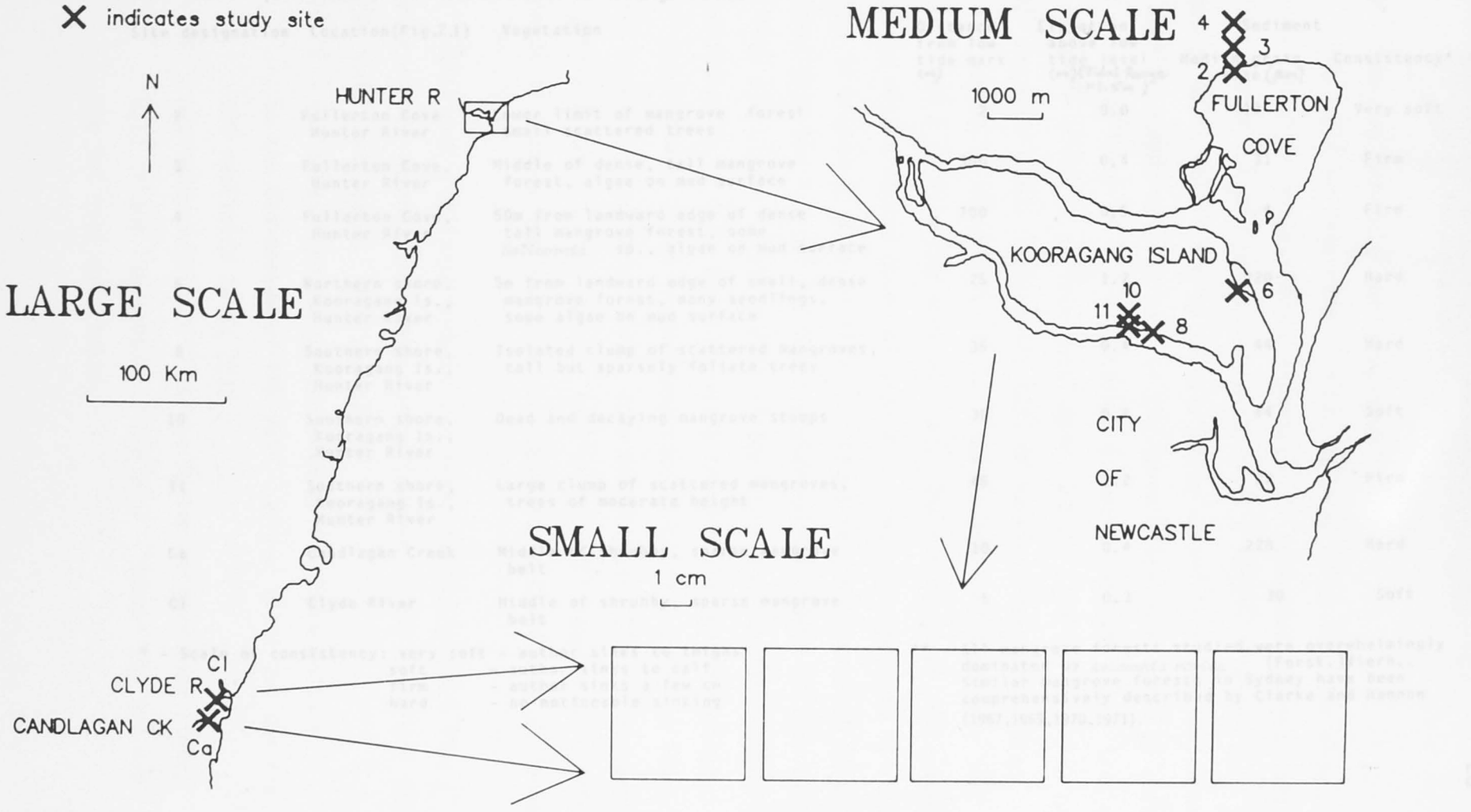


TABLE 2.1 Environmental conditions at study sites

Site designation	Location (Fig. 2.1)	Vegetation	Distance from low tide mark (m)	Elevation above low tide level (m) (Tidal Range = 1.5m)	Sediment: Median grain size (μm)	Sediment: Consistency*
2	Fullerton Cove Hunter River	Lower limit of mangrove forest small scattered trees	2	0.0	19	Very soft
3	Fullerton Cove, Hunter River	Middle of dense, tall mangrove forest, algae on mud surface	300	0.4	31	Firm
4	Fullerton Cove, Hunter River	50m from landward edge of dense tall mangrove forest, some *Salicornia* sp., algae on mud surface	700	0.5	4	Firm
6	Northern shore, Kooragang Is., Hunter River	5m from landward edge of small, dense mangrove forest, many seedlings, some algae on mud surface	25	1.2	220	Hard
8	Southern shore, Kooragang Is., Hunter River	Isolated clump of scattered mangroves, tall but sparsely foliate trees	35	0.4	44	Hard
10	Southern shore, Kooragang Is., Hunter River	Dead and decaying mangrove stumps	35	0.4	44	Soft
11	Southern shore, Kooragang Is., Hunter River	Large clump of scattered mangroves, trees of moderate height	45	1.2	12	Firm
Ca	Candlagan Creek	Middle of shrubby, sparse mangrove belt	10	0.4	228	Hard
Cl	Clyde River	Middle of shrubby, sparse mangrove belt	5	0.3	30	Soft

* - Scale of consistency: very soft - author sinks to thighs
soft - author sinks to calf
firm - author sinks a few cm
hard - no noticeable sinking

** - All mangrove forests studied were overwhelmingly dominated by *Avicennia marina* (Forsk.)Vierh.. Similar mangrove forests in Sydney have been comprehensively described by Clarke and Hannon (1967,1969,1970,1971).

2.1.2 Sampling Schedule and Techniques

The sampling data came from two sources which used the same sampling technique but different apparatus. I collected the mud samples from the Hunter estuary whilst employed under a Marine Sciences and Technology Grant supervised by Dr W.L. Nicholas and Professor C. Bryant. Five replicate samples from each of the seven sites were taken by pushing a circular corer of 1.5 cm internal diameter into the mud. Samples were taken in a row, 1 cm from each other, within a period of three days in late December 1981. Subsequent sets of samples were taken, also within a period of three days, in late March, June and September 1982 in parallel rows 5 cm from the previous row. These subsequent replicates were taken with a square corer of side 5 cm, but each core was bisected from top to bottom to give an effective cross-sectional area of 12.5 cm^2 (compared with the 4.9 cm^2 for the circular corer). Sets of five replicates from the single sites in each of the Clyde and Candlagan estuaries were collected by Dr W.L. Nicholas using the circular corer described above. Samples were taken in the same spatial configuration as those from the Hunter during early April, July and October 1979 and January 1980, generally within four days of each other. All samples were taken to a depth of 6 cm during low tide and immediately fixed with 5% formalin.

Individual replicate samples are identified throughout this thesis by a code which allows easy identification of the place and time that the sample was taken. For example:

Cl III E was taken from the single site at the Clyde estuary (Cl) in the 3rd season of the year - winter (III) and was the 5th replicate taken (E);

3 I A was taken from site 3 in the Hunter estuary (see Figure 2.1) in the 1st season of the year - summer (I) and was the 1st replicate taken.

2.1.3 Extraction of Nematodes and Enumeration

The nematodes from each sample were extracted using a combination of sedimentation, sieving and centrifugation (Appendix 2). A portion of each sample was mounted on microscope slides in anhydrous glycerol for identification. One hundred nematodes from a measured but randomly chosen proportion of each of the samples from the Hunter were mounted. All nematodes from half of each sample from the Clyde and Candlagan estuaries were mounted. The nematodes on each slide were sorted and counted by species but most of the species could only be assigned generic names because taxonomic knowledge of Australian marine nematodes is poor. The sex and reproductive status of individuals was noted where possible.

The numbers of each species in the subsamples were divided by the proportion of the entire sample counted to estimate the numbers of each species in the whole sample. To allow for the different sample sizes in later comparisons, the density of each species was expressed per cm^2 surface area since it is widely used in comparisons of meiofaunal density. Although volume is more ecologically meaningful as a measure of the distances between individual animals, it is not easily measured in the wet, easily suspended sediment. Weight is an unsuitable measure because the density of the sediment varies according to water holding capacity, grain size, root density and many other factors. Measurements of both volume and weight of the Hunter River samples were taken for comparison of results obtained using different measures of density (Appendix 5).

The method used to estimate the density assumes that the species composition and population structure of the subsample were representative of the entire sample. The validity of this assumption was tested by identifying and counting all nematodes from four of the replicate samples and comparing the actual number with those estimated from sub-sampling. Using either 4.9 or 12.5 cm^2 samples from the Hunter, the

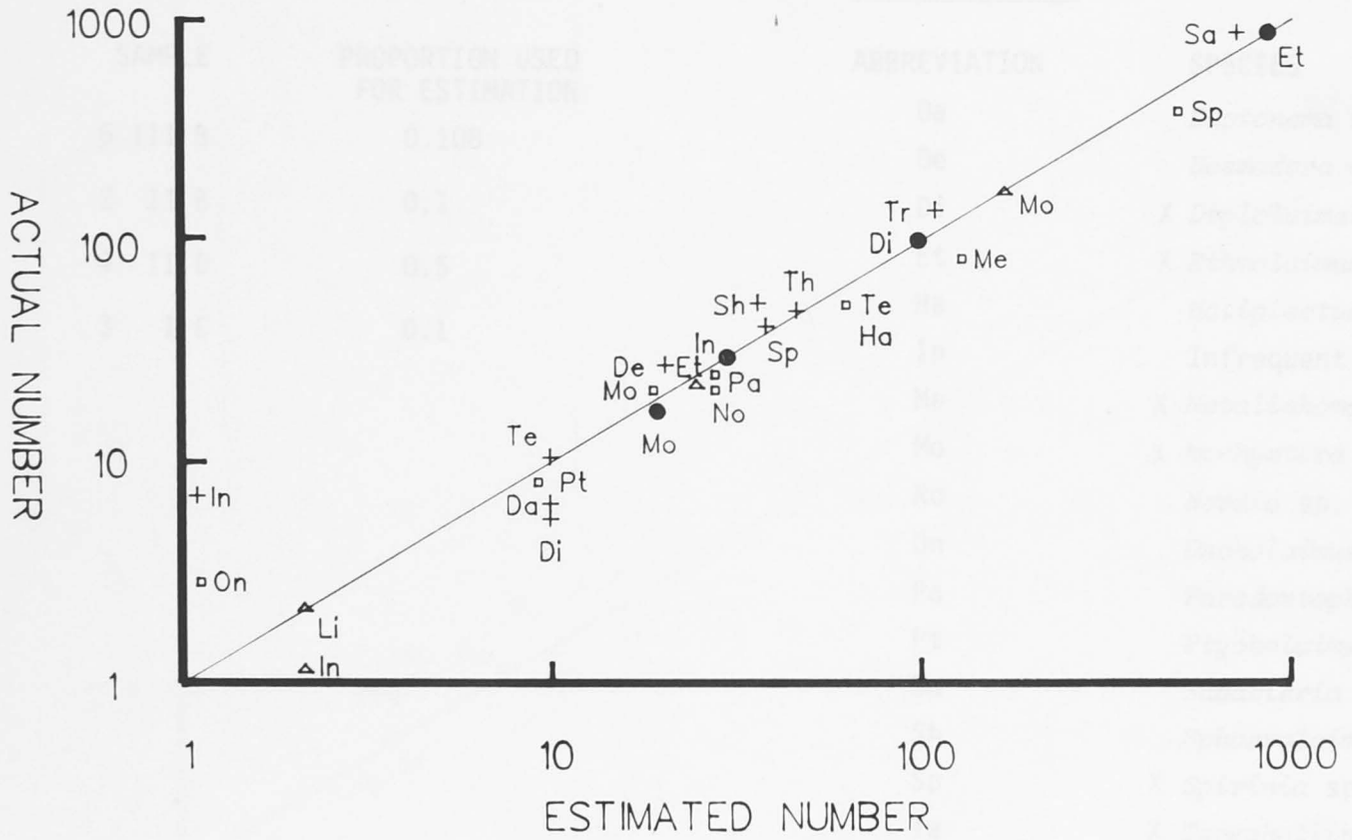
deviation of projected densities from actual counts was modest (Figure 2.2). Of the many species represented in the test samples, there was no consistent bias in any particular size or taxonomic group. The percentage deviation in density decreased as larger proportions of the sample were counted (Figure 2.2), but the relative abundance of common species was always very close to that predicted (Figure 2.3). These two observations suggest that the discrepancies between observed and projected densities arose from small errors in measuring and calculating the proportion of the whole sample counted. Although the remainder of the Clyde and Candlagan samples were unavailable to test, any variations should be small given that half the samples were counted.

2.2 *STATISTICAL ANALYSIS*

Two non-parametric statistical methods - ordination analysis and cluster analysis, were the major statistical methods used in this study. Although these methods produce statistical inferences less powerful than some other methods, neither relies on assumptions that the structure and spatial distribution of the population under study conforms to a particular statistical model: this is important because the distribution of the nematodes in this study did not conform to any standard statistical distribution (Appendix 1). As both methods are quite complex, a full discussion of each is relegated to Appendix 3, however to aid in the interpretation of results, a brief description of each is given here.

Suppose that various numbers of 10 species of nematodes are found in three different samples (Table 2.2). Each species may be thought of as a point in a 3-dimensional space defined by co-ordinates representing the number of animals in each of the three samples (Figure 2.4). Several aspects of the distribution of these points can reveal much about the nature of the populations from which the samples and species came.

FIGURE 2.2 ACCURACY OF ESTIMATED NUMBERS OF NEMATODE SPECIES



KEY TO SAMPLE ORIGIN

SYMBOL	SAMPLE	PROPORTION USED FOR ESTIMATION
○	6 III B	0.108
+	2 II B	0.1
⌓	4 II D	0.5
●	3 I C	0.1

KEY TO SPECIES

ABBREVIATION		SPECIES
Da		*Daptonema* sp.
De		*Desmodora cazca*
Di	X	*Diplolaimelloides* sp.
Et	X	*Ethmolaimus* sp.
Ha		*Haliplectus* sp.
In		Infrequent species
Me	X	*Metalinhomoeus* sp.
Mo	X	*Monhystera* sp.
No		*Nordia* sp.
On		*Oncholaimus* sp.
Pa		*Parodontophora* sp.
Pt		*Ptycholaimellus* sp.
Sa		*Sabatieria* sp.
Sh		*Sphaerolaimus* sp.
Sp	X	*Spirinia* sp.
Te	X	*Terschellingia longicaudata*
Th		*Theristus interstitialis*
Tr		*Tripyloides* sp.

X indicates more than 1 record

FIGURE 2.3 CONCORDANCE OF THE PROPORTIONS OF COMMON SPECIES IN SUB–SAMPLES & WHOLE SAMPLES

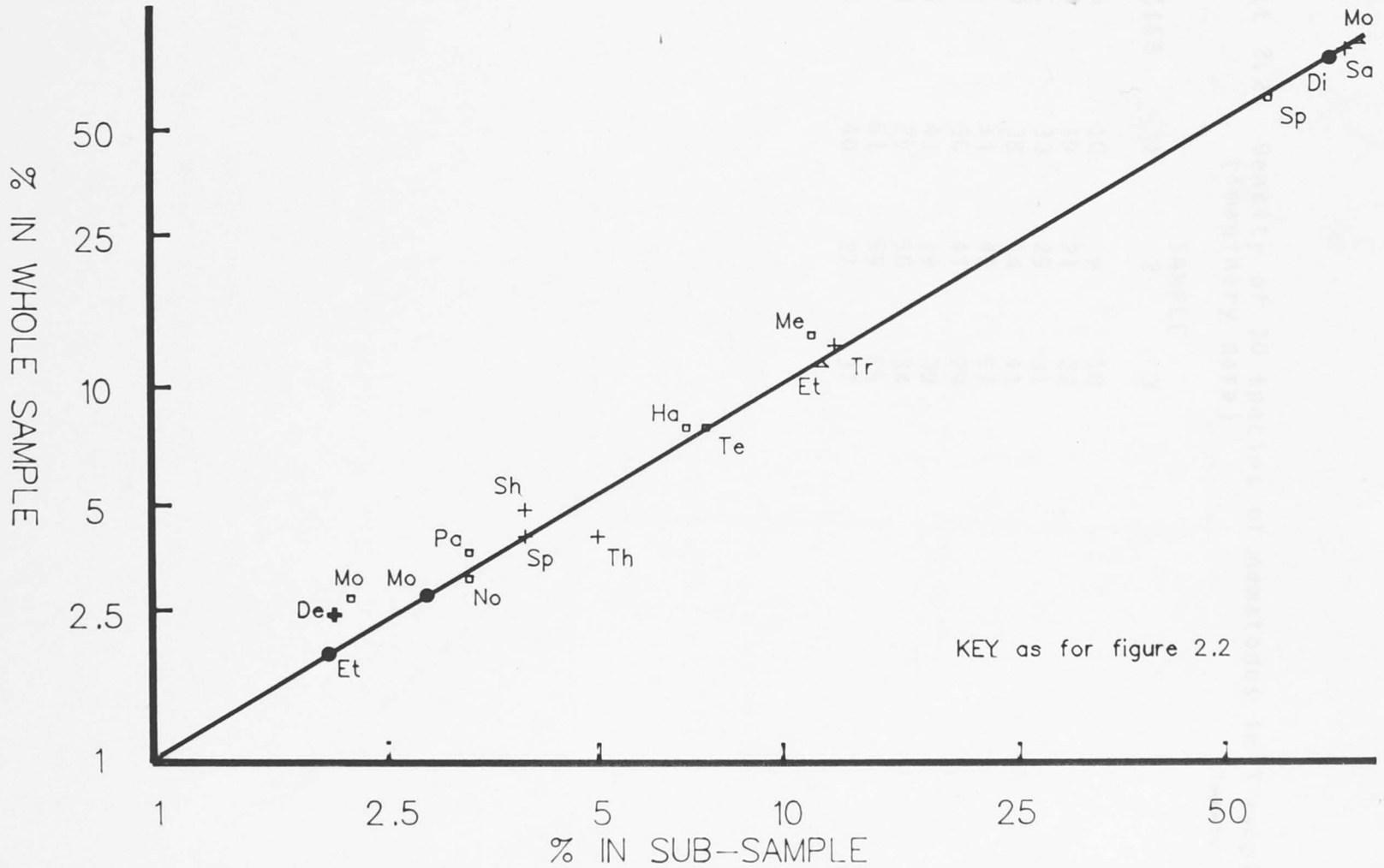
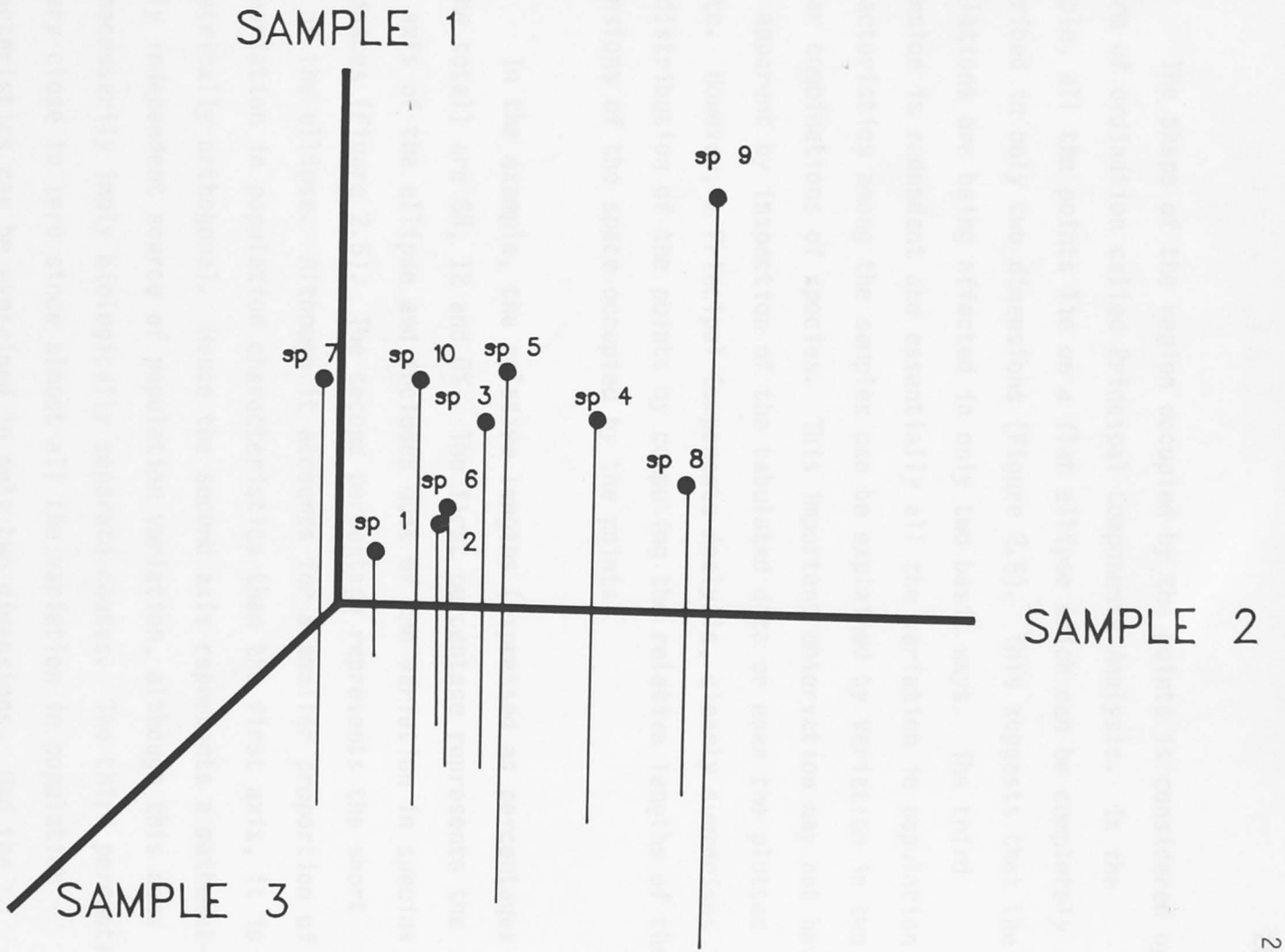


TABLE 2.2 Density of 10 species of nematodes in 3 samples (imaginary data)

SPECIES	SAMPLE 1	2	3
A	10	9	10
B	19	21	22
C	33	29	31
D	38	44	41
E	51	45	57
F	30	41	29
G	41	19	39
H	29	50	34
I	61	59	65
J	40	27	37

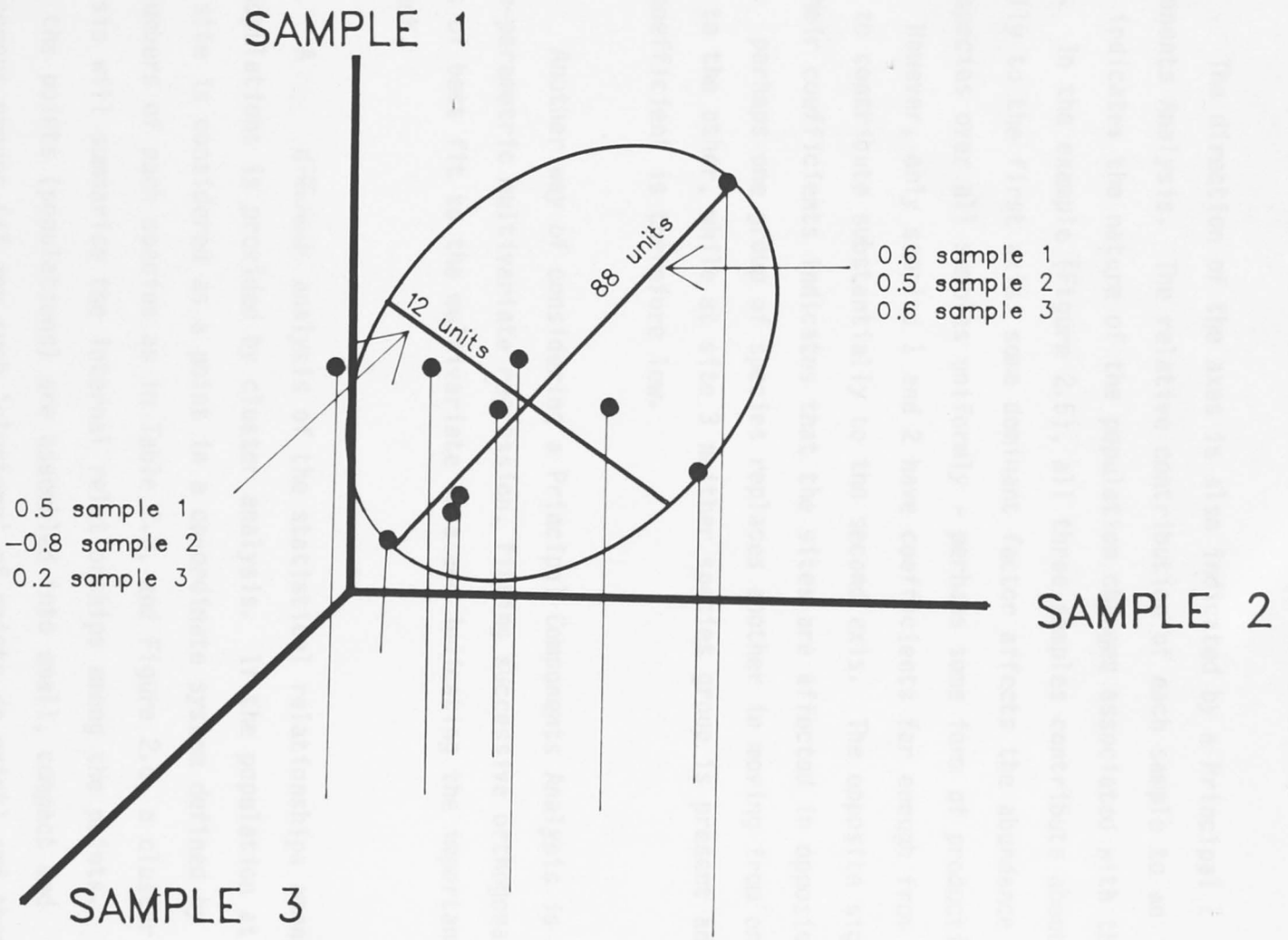
FIGURE 2.4 SPECIES AS POINTS IN SAMPLE SPACE



The shape of the region occupied by the points is considered by a form of ordination called Principal Components Analysis. In the example, all the points lie on a flat ellipse which can be completely described in only two dimensions (Figure 2.5). This suggests that the populations are being affected in only two basic ways. The third dimension is redundant and essentially all the variation in population characteristics among the samples can be explained by variation in two linear combinations of species. This important observation may not have been apparent by inspection of the tabulated data or even the plotted points. However, a Principal Components Analysis, clearly summarises the distribution of the points by computing the relative lengths of the dimensions of the space occupied by the points.

In the example, the relative lengths (expressed as percentages of the total) are 88, 12 and 0%. The first percentage represents the long axis of the ellipse and includes most of the variation in species abundances (Figure 2.5). The second percentage represents the short axis of the ellipse. Although it accounts for a smaller proportion of the variation in population characteristics than the first axis, it is geometrically orthogonal. Hence the second axis represents a mathematically independent source of population variation, although this does not necessarily imply biologically separate causes. The third percentage is very close to zero since almost all the variation in population characteristics can be explained in only two dimensions. Had the populations been overwhelmingly controlled by a single factor, all the points would lie on or near a single straight line and a single axis would account for all the variation. The remaining axes would be close to zero. Conversely, if three factors influenced the populations to a similar extent and the points occupied a sphere, all axes would be about equal. This would also occur if the populations in the three samples were all statistically independent of each other.

FIGURE 2.5 ELLIPSE DESCRIBING SPECIES POINTS IN SAMPLE SPACE



The direction of the axes is also indicated by a Principal Components Analysis. The relative contribution of each sample to an axis indicates the nature of the population changes associated with that axis. In the example (Figure 2.5), all three samples contribute about equally to the first axis: some dominant factor affects the abundance of all species over all samples uniformly - perhaps some form of productivity. However, only samples 1 and 2 have coefficients far enough from zero to contribute substantially to the second axis. The opposite signs of their coefficients indicates that the sites are affected in opposite ways: perhaps one group of species replaces another in moving from one site to the other, while at site 3 neither species group is present and the coefficient is therefore low.

Another way of considering a Principal Components Analysis is as a non-parametric multivariate regression, fitting successive orthogonal lines of best fit to the multivariate data and indicating the importance of each.

A different analysis of the statistical relationships among the populations is provided by cluster analysis. If the population at each site is considered as a point in a co-ordinate system defined by the numbers of each species as in Table 2.3, and Figure 2.6, a cluster analysis will summarise the internal relationships among the points. First the points (populations) are assembled into small, compact and homogeneous groups (if any such 'clusters' of points do exist) and then into successively larger, more diffuse groups (Figure 2.7). At each stage of the process of grouping the points the cluster analysis indicates the successively larger distances between the points in a cluster. The best and conventional way to summarise this process is to display these population relationships by a dichotomous dendrogram (Figure 2.8). In a dendrogram the samples, at the ends of the 'twigs', join to form larger and larger 'branches' or groups at a 'height' equal to the distance between the two joining groups.

TABLE 2.3 Density of 3 species of nematodes in 10 samples (imaginary data)

	SPECIES		
SAMPLE	A	B	C
1	10	36	37
2	1	49	2
3	45	15	18
4	32	37	38
5	15	37	30
6	43	17	17
7	41	19	18
8	29	30	30
9	11	40	40
10	26	35	36

FIGURE 2.6 SAMPLES AS POINTS IN SPECIES SPACE

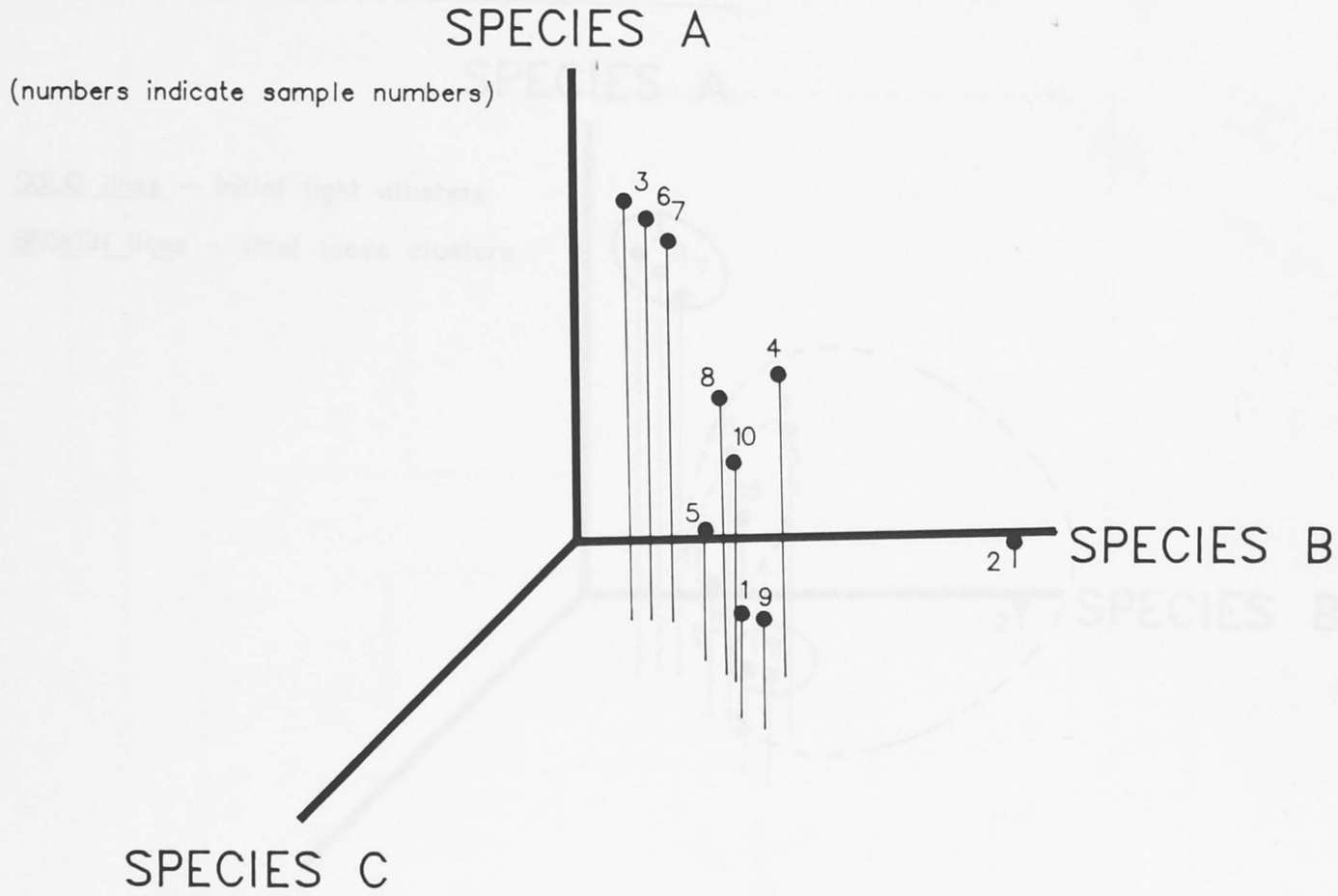


FIGURE 2.7 CLUSTERING OF SAMPLES IN SPECIES SPACE

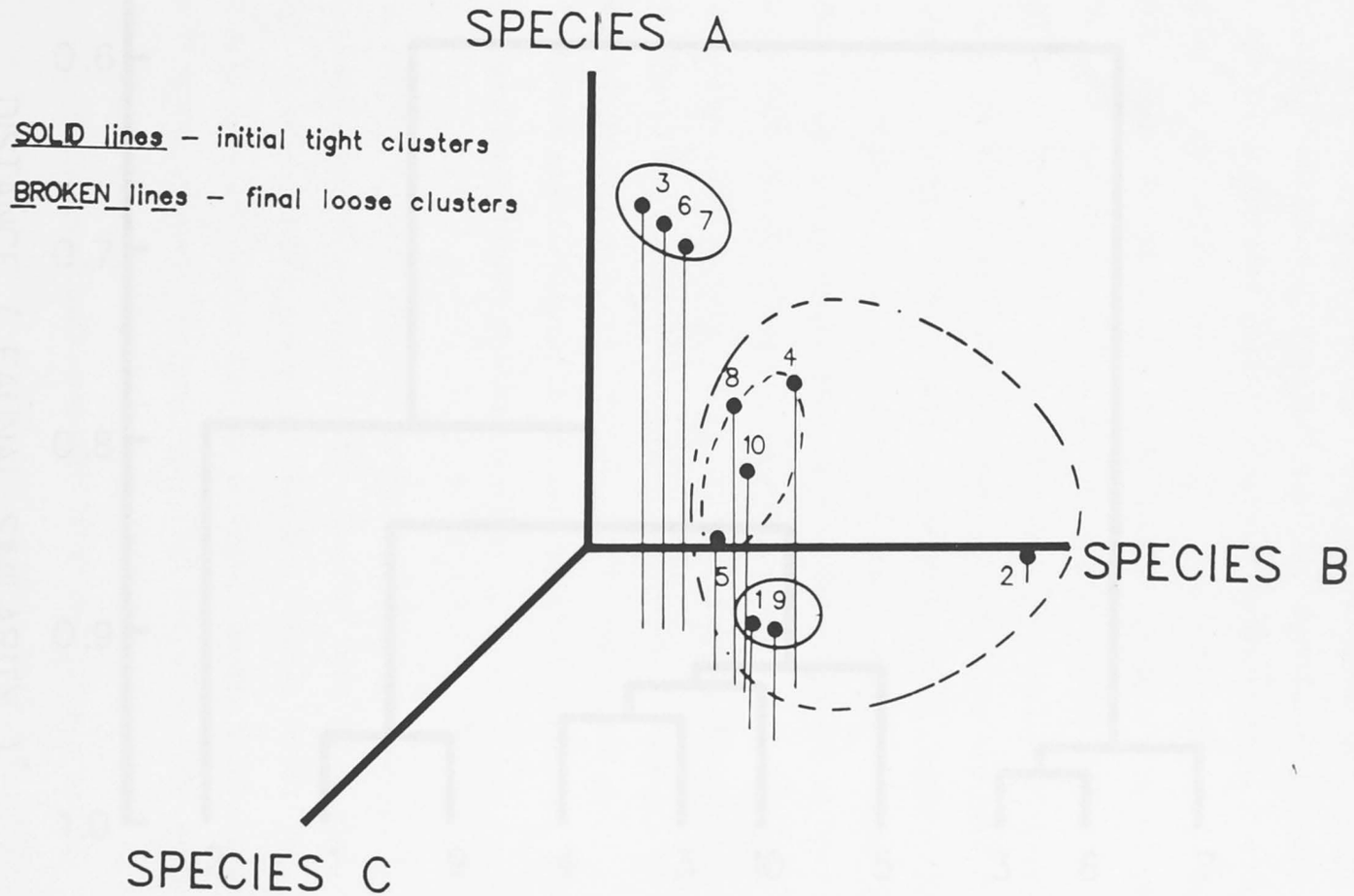
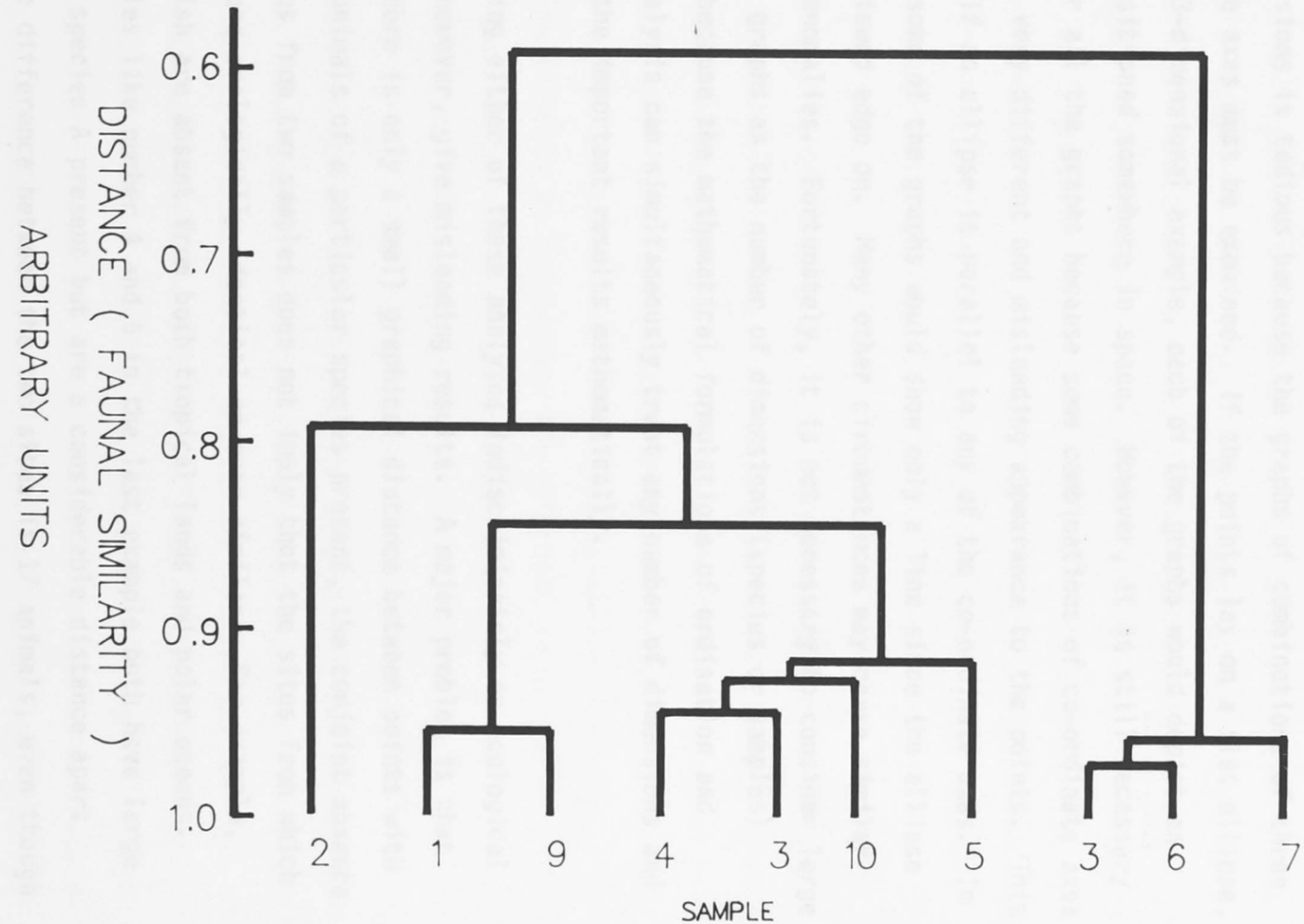


FIGURE 2.8 DENDROGRAM OF SAMPLE CLUSTERING (imaginary data)



The example in the above demonstration of statistical methods uses only three dimensions for clarity, however these analyses apply equally well, and indeed are of greatest benefit, when there are many samples and species to be considered. Graphical consideration of even four dimensions is tedious because the graphs of combinations of three co-ordinate axes must be examined. If the points lay on a flat ellipse, as in the 3-dimensional example, each of the graphs would depict an ellipse positioned somewhere in space. However, it is still necessary to consider all the graphs because some combinations of co-ordinate axes may give a very different and misleading appearance to the points. This can occur if an ellipse is parallel to any of the co-ordinate axes. In this case some of the graphs would show only a line since the ellipse would be viewed edge on. Many other circumstances may cause similar graphical anomalies. Fortunately, it is not necessary to consider large numbers of graphs as the number of dimensions (species or samples) increases because the mathematical formulations of ordination and cluster analysis can simultaneously treat any number of dimensions and summarise the important results mathematically.

Using either of these analyses indiscriminately on ecological data can, however, give misleading results. A major problem is that although there is only a small graphical distance between points with few or no animals of a particular species present, the conjoint absence of a species from two samples does not imply that the sites from which they came are ecologically identical or even similar. For example, tropical fish are absent from both tropical lands and polar oceans. Also, samples like number 4 and 5 in the last example both have large numbers of species A present but are a considerable distance apart because the difference between the two sites is 17 animals, even though this is proportionally small (Figure 2.6). However, sites 1 and 2 are much closer together because the difference in the numbers of species A is only 9 animals, even though this is a 10-fold difference and less certain because of the smaller numbers of animals present. These eco-

logically undesirable properties of using Euclidean distance as the measure of ecological similarity between points necessitated using a different measure of similarity. The Bray-Curtis similarity coefficient was used since it was designed specifically for ecological work. This coefficient ignores joint absences and stresses joint presences, giving a weight to each species proportional to the number of animals present. Thus in the last example species A contributes about 20% to the similarity between sites 4 and 5 where 47 animals are present but only about 8% to the similarity between sites 1 and 2 where only 11 are present. This weighting of abundant species also diminishes the effect of any sampling errors on rare species since poorly represented species contribute little to the similarity of two sites.

The Bray-Curtis similarity coefficient, however, differs in a few minor but statistically important properties from Euclidean distance. The differences necessitate the use of a slightly different form of ordination called Principal Co-ordinate Analysis. Principal Co-ordinate Analysis is a more general form of a Principal Component Analysis, incorporating features to accommodate the different properties of a similarity coefficient. Cluster analysis is unaffected by the measure used to quantify the likeness of sites.

Ordination methods may also be used to summarise the ecological relationships among the different species by comparing their distributions. However, for reasons explained later, the distributions of species were compared between the different sites, not the individual samples. Because the total densities of each species at each site have different statistical properites to the densities of species in individual samples, Principal Component Analysis was used rather than Principal Co-ordinate Analysis. The two ordination methods are somewhat similar, however Principal Component Analysis operates directly on the densities

of each species and hence does not require computation of a measure of the similarity of species distributions. More details are given in Appendix 3.

All analyses were calculated by the Univac 1100/82 computer at the Australian National University. Data manipulation and non-standard analyses used Fortran 77 programs and IMSL subroutines; standard analyses used Genstat 4.01 programs. I wrote all programs and thoroughly tested them before use.

2.3 *RELIABILITY OF SAMPLING DATA*

To draw valid statistical inferences, sampling data must accurately and consistently represent the true populations. Hence a brief examination of possible sources of artifact is detailed below.

a) *Extraction Procedure*

The efficiency of the method of extracting nematodes from substrate was examined by extracting the nematodes from samples containing known numbers of animals. Two species common in the field samples, one small and the other of moderate size, were obtained from laboratory cultures and introduced in separate 75 cm^2 volumes of mud which had been defaunated by extracting the animals and then freezing and thawing twice. The mud was from the site in the middle of the range of median grain sizes (site 13) and was equal in volume to the square corer samples. It was shaken in a plastic cup with lid to distribute the nematodes throughout the sediment and then processed in exactly the same manner as the field samples.

Retrieval rates were quite high for both species (Table 2.4), but more importantly there was little variation between the replications for a single species, irrespective of the initial density.

TABLE 2.4 Recovery rates of nematodes

SPECIES	No. IN	No. OUT	% OUT	
Diplolaimelloides sp.	1024	530	51.7	49.1
	565	278	49.2	
	508	239	47.0	
	258	125	48.4	
Paracyatholaimus sp.	38	23	60.5	

The reliability of the extraction method is also supported by the field data. Some very small and inconspicuous species were successfully extracted and very large numbers of nematodes were retrieved from the sediment.

b) *Number of Replicate Samples Representing a Site*

How well five replicate samples represent a site was partially evaluated by examining the mean number of species added to the species list for a site by taking additional samples. Additional samples to the five normally taken to represent the sites were likely to add few extra species and little extra data about the populations at a site (Figure 2.9). However, no complete evaluation of the effect of additional sampling is possible since a complete analysis would involve taking multiple sets of replicates as well as a set of very large samples equal in volume to all the replicates - a major study in itself. Also, many additional factors complicate the problem, particularly variation within the replicates themselves and variation over time. Such variation is addressed as a major part of this study: the results imply that five replicates do adequately represent a site at one particular time (section 3.1).

c) *Effect of Different Operators and Sample Sizes*

The comparability of the samples collected in different apparatus or by different operators is assessed as part of the results of the cluster analysis reported in section 3.1, and shown in Figure 3.3. Neither sample size nor operator caused an overwhelming pattern in the data. This is clearly seen in representative sections of the dendrogram where samples of different sizes and those taken by different operators were intermingled rather than in discrete groups (Figure 2.10).

FIGURE 2.9 NUMBER OF NEW SPECIES ADDED BY ADDITIONAL SAMPLING

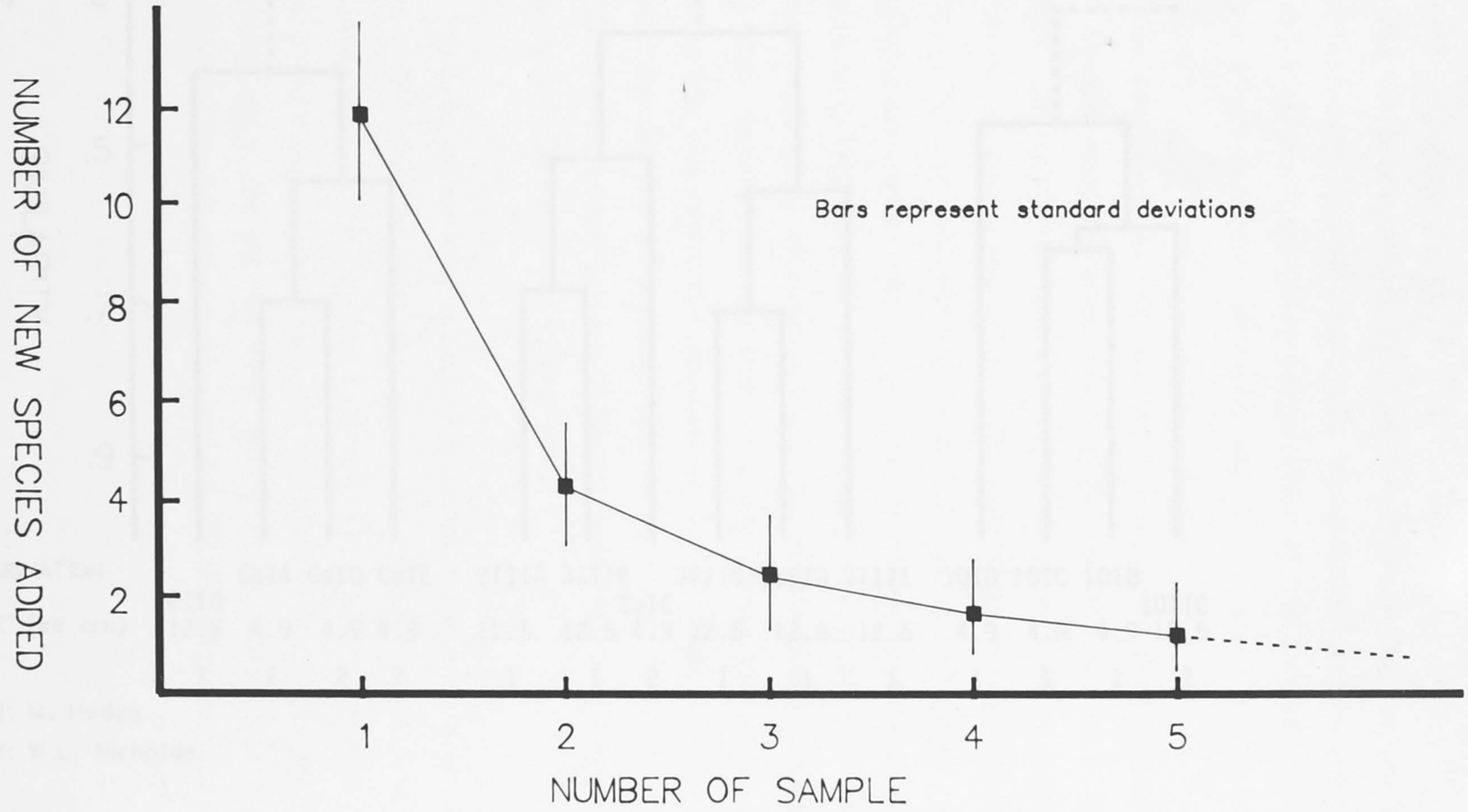
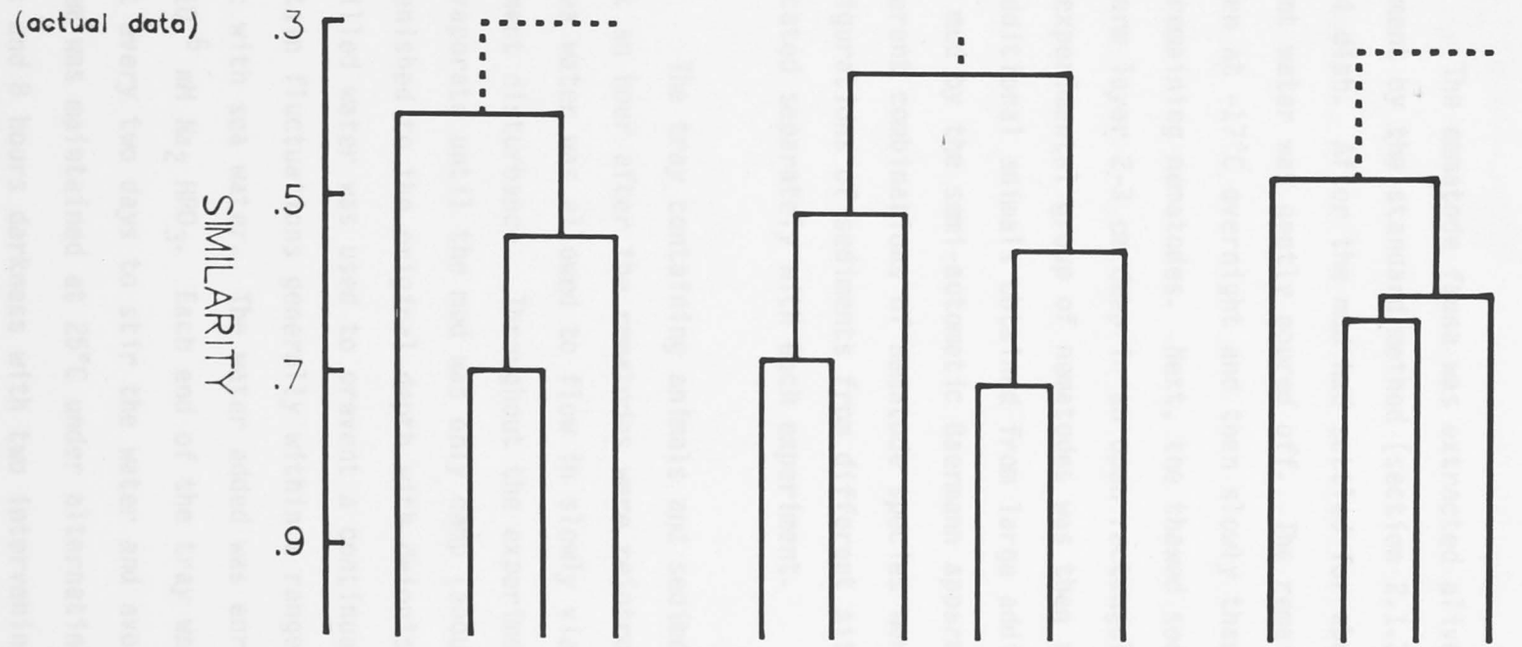


FIGURE 2.10 PORTIONS OF DENDROGRAM SHOWING NEGLIGIBLE EFFECTS OF OPERATOR & SAMPLE SIZE ON FAUNA



operator 1: M. Hodda

operator 2: W.L. Nicholas

2.4 *THE LABORATORY MICROCOSM*

The mechanisms by which the different ecological processes affected the nematode populations were investigated using a laboratory system which allowed controlled manipulation of the nematode populations while retaining conditions somewhat comparable to the field.

The nematode fauna was extracted alive from large quantities of sediment by the standard method (section 2.1.3) and kept aside in a petri dish. After the mud had settled for about an hour, any supernatant water was gently poured off. The remaining sediment was deep frozen at -17°C overnight and then slowly thawed to 20°C twice, to kill any remaining nematodes. Next, the thawed sediment was placed in a uniform layer 2-3 cm deep in an open rectangular tray 55 x 44 x 8 cm. The experimental group of nematodes was then reintroduced, supplemented by additional animals obtained from large additional quantities of the same mud by the semi-automatic Baermann apparatus (Thorne 1961). Different combinations of nematode species were used in various spatial configurations of sediments from different sites and estuaries, as indicated separately with each experiment.

The tray containing animals and sediment was initially inundated about an hour after the nematodes were reintroduced. About 1 cm depth of sea water was allowed to flow in slowly via a very thin tube to avoid sediment disturbance. Throughout the experiments the water was allowed to evaporate until the mud was only damp (about 4-6 days) and then replenished to the original depth with deionised distilled water. Distilled water was used to prevent a continual increase in salinity and maintain fluctuations generally within a range of hypersaline to isotonic with sea water. The water added was enriched with 10^{-4} mM $NaNO_3$ and 10^{-5} mM $Na_2 HPO_3$. Each end of the tray was gently lifed a few cm about every two days to stir the water and avoid stagnation. The entire system was maintained at 25°C under alternating periods of 15 hours light and 8 hours darkness with two intervening periods of 30 minutes intergradation.

The fauna in the trays was sampled using an 8 cm length of cylindrical tube of 4.7 cm^2 cross-sectional area. This area is almost identical to the circular corer used to take field samples. The sampler was pushed into the mud until flush with the bottom of the tray, the mud within the tube was then sucked out via an 8 mm internal diameter tube into a vacuum flask by a venturi pump. A little distilled water was sucked through the tube to wash out any remaining mud and the contents of the flask were washed into a plastic sample cup. Any mud adhering to the internal wall of the sampler after withdrawal was also washed into the cup. The sample was then processed by the standard method (Appendix 1) except that decantation was unnecessary before centrifugation because the samples were so small. The nematodes were counted in the petri dish, not mounted on slides. All samples were taken when the water level was low.

CHAPTER 3

THE RELATIVE IMPORTANCE OF DETERMINISTIC AND STOCHASTIC PROCESSES AND THE SCALES ON WHICH THEY OPERATE

3.1 *SIMPLE PATTERNS OF FAUNAL GROUPS AND DISCONTINUITIES*

3.1.1 Introduction

The difference between populations controlled by deterministic and stochastic processes is pattern. Strong patterns in the population characteristics of different samples indicate that deterministic pro cesses control the population. Random assortments of species at indeterminate densities indicate that chance and stochastic processes are most important. Hence the presence or absence of sharp discontinuities in population characteristics between groups of samples with internally homogeneous populations is a strong indication of which processes predominate. Cluster analysis of all the individual replicate samples can indicate if there is such a pattern and how strong it is. Cluster analysis can also indicate which scale of sampling encompasses the most important changes in population characteristics. The dendrogram produced by a cluster analysis can show this by the size and nature of any groups of samples identified. The combination of the strength and nature of any pattern in the population characteristics of the samples can thus differentiate which ecological process is predominant and on which scale it operates (Figures 3.1 and 3.2). These patterns cover all extreme possibilities, however intermediate configurations are possible. If more than one ecological process or scale is involved, the constituent patterns should still be discernable. If this is the case, cluster analysis can give a qualitative estimate of the importance of the different processes and scales according to the relative strengths of the patterns in the dendrogram.

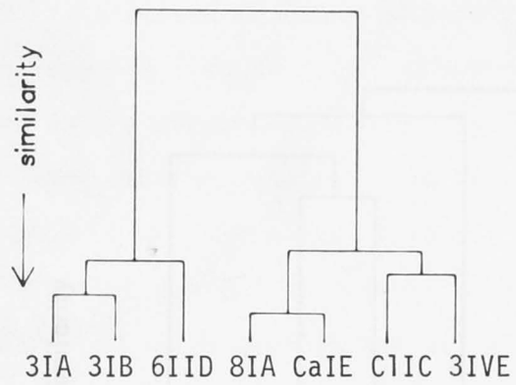
3.1.2 Method

A cluster analysis was carried out by group average sorting as described in Appendix 3c.

FIGURE 3.1 DENDROGRAM PATTERNS PRODUCED BY DETERMINISTIC PROCESSES

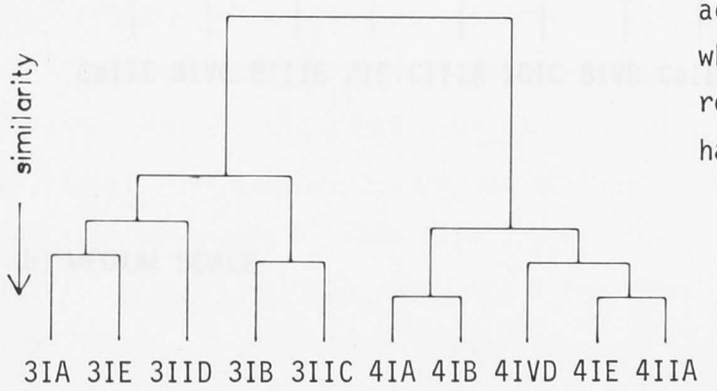
(examples only)

a) SMALL SCALE



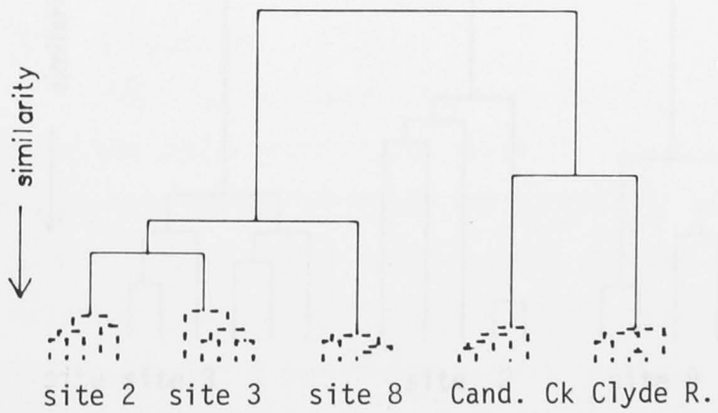
Unrelated samples group discretely according to whichever small scale factor is important.

b) MEDIUM SCALE



Samples group discretely according to the site from which they came. The relationships among the sites have simple explanations.

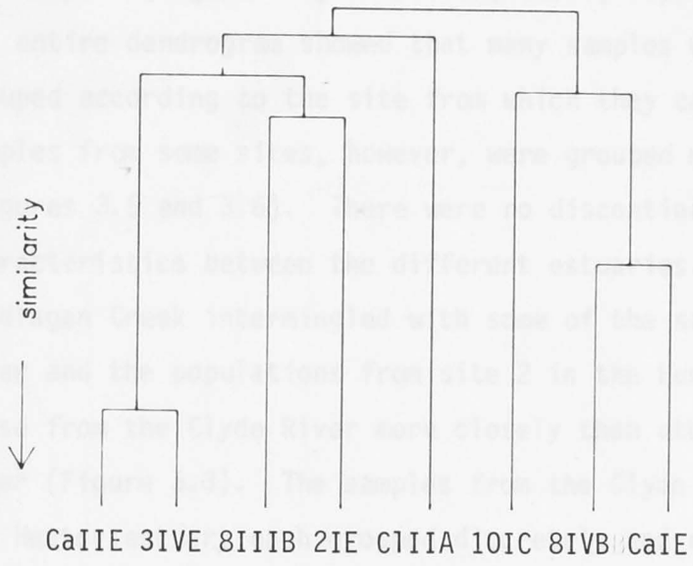
c) LARGE SCALE



Samples group in almost any fashion but the south coast estuaries are very different from the Hunter estuary.

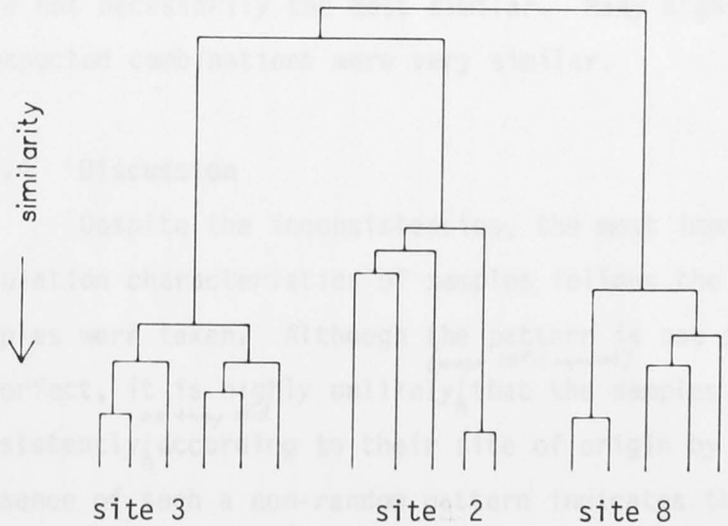
FIGURE 3.2 DENDROGRAM PATTERNS PRODUCED BY STOCHASTIC PROCESSES

a) SMALL SCALE



No consistent pattern in grouping individual samples, sites or estuaries. Different samples are grouped at very different levels of population similarity.

b) MEDIUM SCALE



Samples group according to site, but the relationships among the sites cannot be related to any measurable factor.

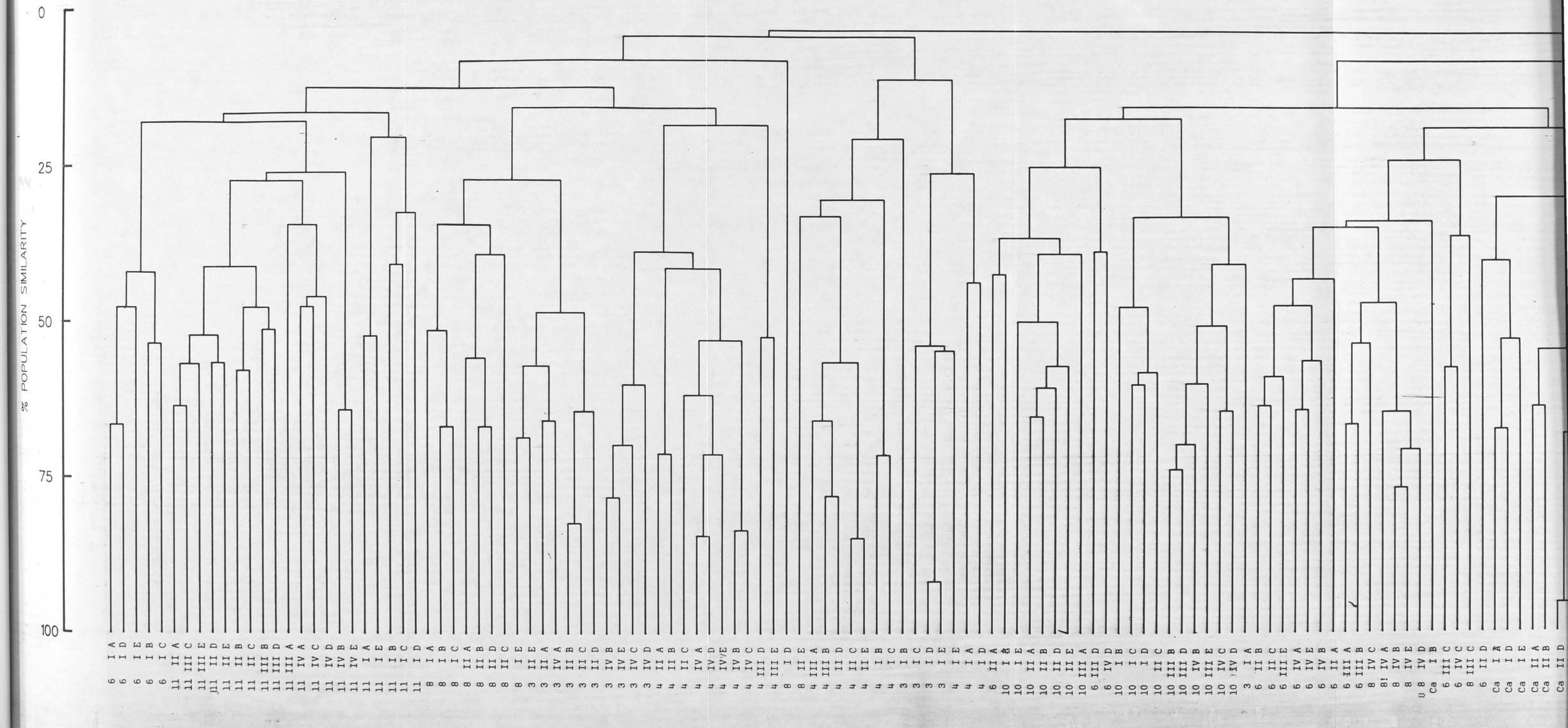
3.1.3 Results

The configuration of the dendrogram produced by the cluster analysis showed no clear pattern in the population characteristics of the samples (Figure 3.3). However, small, representative portions of the entire dendrogram showed that many samples were partially and loosely grouped according to the site from which they came (Figure 3.4). The samples from some sites, however, were grouped more diffusely than others (Figures 3.5 and 3.6). There were no discontinuities in population characteristics between the different estuaries. The samples from Candlagan Creek intermingled with some of the samples from the Hunter River and the populations from site 2 in the Hunter River resembled those from the Clyde River more closely than other sites in the Hunter River (Figure 3.3). The samples from the Clyde estuary and site 2 in the Hunter estuary each grouped discretely and were together somewhat distinct from all the other samples. However, the similarity among the replicates from site 2 was very variable and the population characteristics of many samples from site 2 were often only marginally more similar to other samples from site 2 than they were to samples taken at other sites. Except at the Clyde River and site 2, neighbouring samples were not necessarily the most similar. Many highly remote samples and unexpected combinations were very similar.

3.1.4 Discussion

Despite the inconsistencies, the most important pattern in the population characteristics of samples follows the site from which the samples were taken. Although the pattern is not strong and is somewhat imperfect, it is highly unlikely (over 10^5:1 against) that the samples would group as consistently as they did according to their site of origin by chance alone. The presence of such a non-random pattern indicates that deterministic processes at least partly control the characteristics of the populations. However, the pattern was not so strong as to indicate that deterministic processes were operating on a single overwhelmingly important scale. The exact importance of the pattern cannot be quantified from cluster

FIGURE 3.3 DENDROGRAM SHOWING CLUSTERING OF ALL SAMPLES



FIGURE

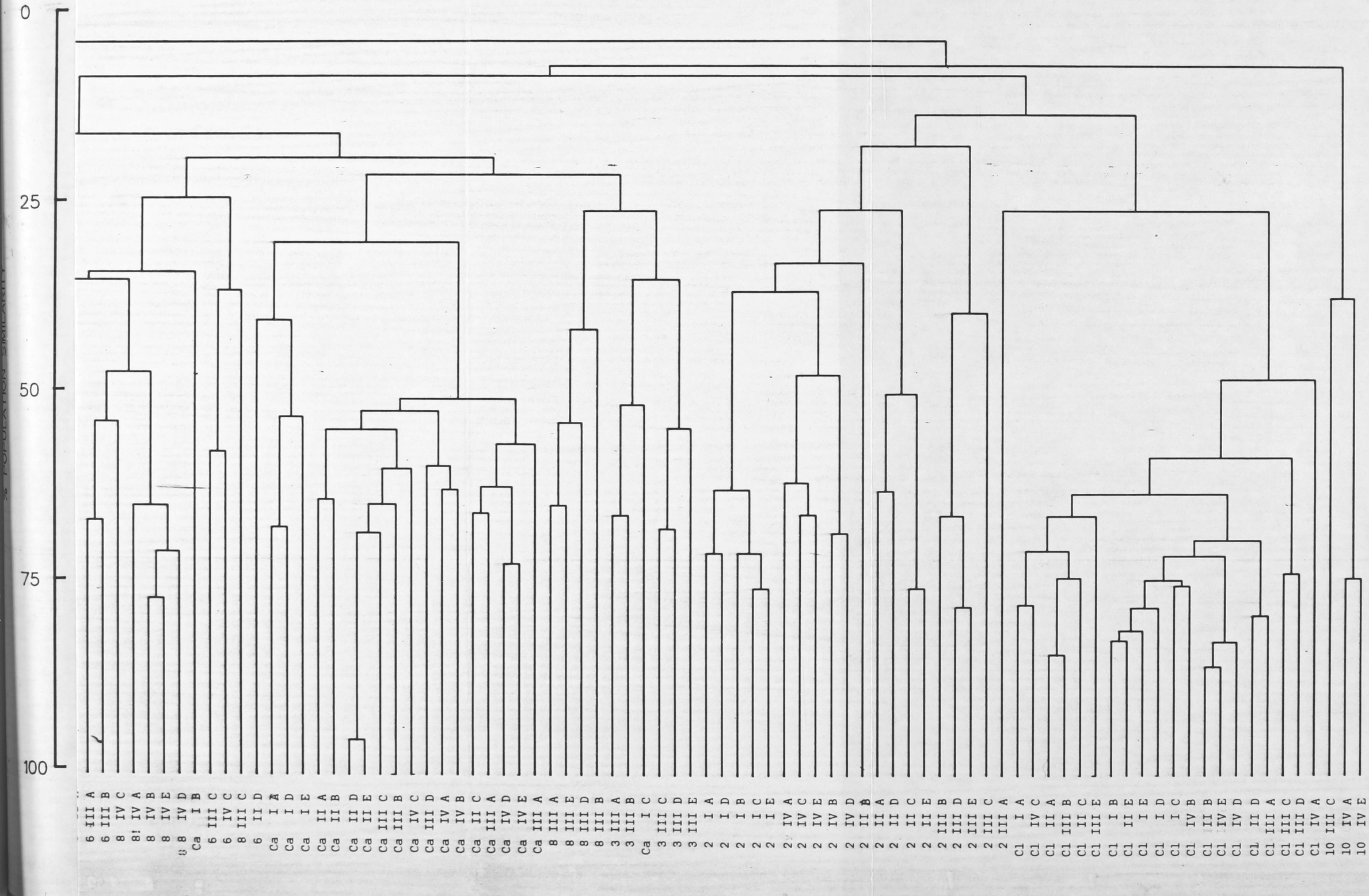
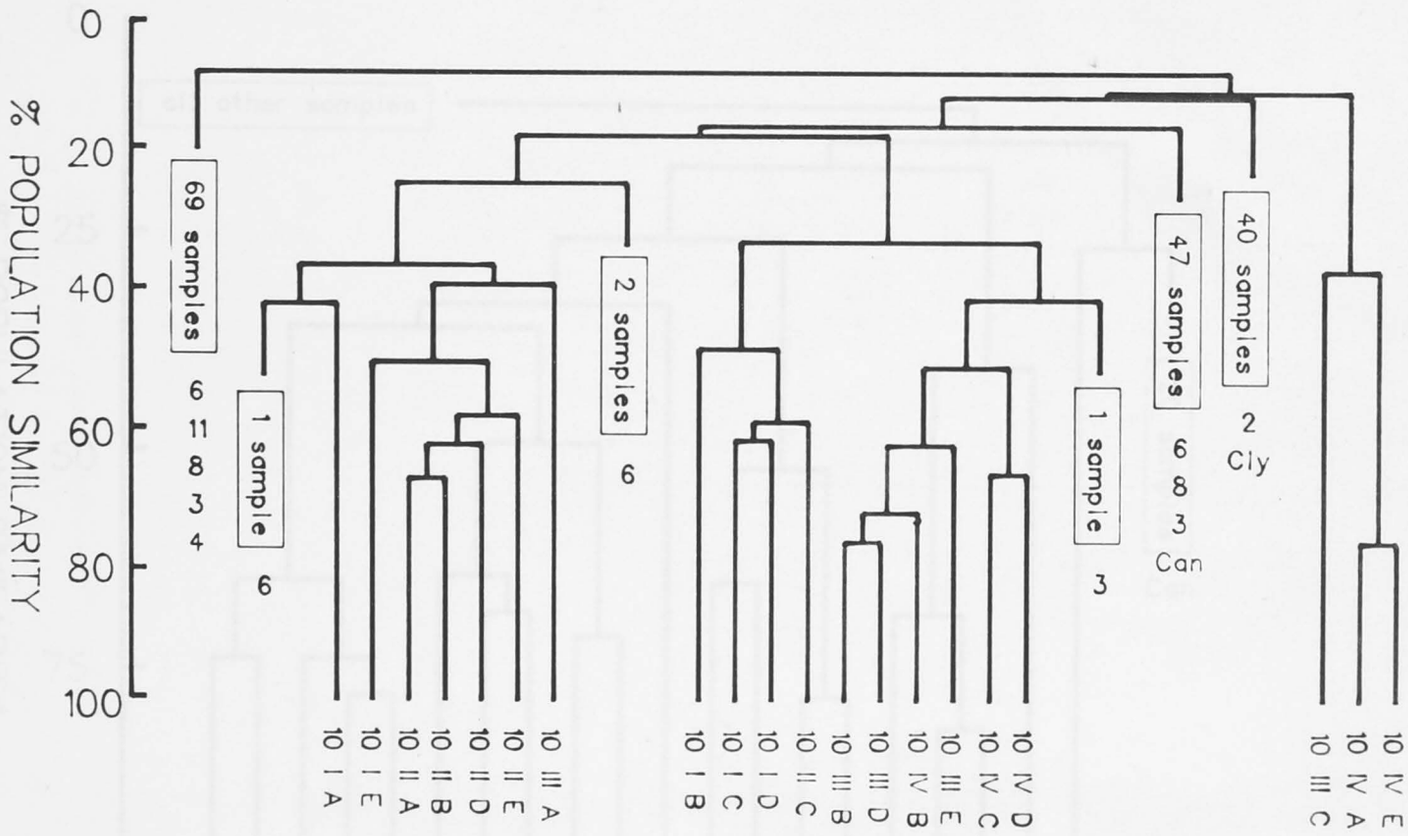

0
25
50
75
100
% POPULATION SIMILARITY
6 III A
6 III B
8 IV C
8! IV A
8 IV B
8 IV E
8 IV D
Ca I B
6 III C
6 IV C
8 III C
6 II D
Ca I A
Ca I D
Ca I E
Ca II A
Ca II B
Ca II D
Ca II E
Ca III C
Ca III B
Ca IV C
Ca III D
Ca IV A
Ca IV B
Ca II C
Ca III A
Ca IV D
Ca IV E
Ca III A
8 III A
8 III E
8 III D
8 III B
3 III A
3 III B
Ca I C
3 III C
3 III D
3 III E
2 I A
2 I D
2 I B
2 I C
2 I E
2 IV A
2 IV C
2 IV E
2 IV B
2 IV D
2 II B
2 II A
2 II D
2 II C
2 II E
2 III B
2 III D
2 III E
2 III C
2 III A
Cl I A
Cl IV C
Cl II A
Cl III B
Cl II C
Cl III E
Cl I B
Cl II E
Cl I E
Cl I D
Cl I C
Cl IV B
Cl III B
Cl IV E
Cl IV D
Cl II D
Cl III A
Cl III C
Cl III D
Cl IV A
10 III C
10 IV A
10 IV E

FIGURE 3.4 SIMPLIFIED DENDROGRAM SHOWING RELATIONSHIPS AMONG SAMPLES FROM SITE 10



Boxes contain the number of samples on each incomplete branch.
Numbers underneath boxes indicate the sites from which the samples came.

FIGURE 3.5 SIMPLIFIED DENDROGRAM SHOWING RELATIONSHIPS AMONG SAMPLES FROM SITE 2

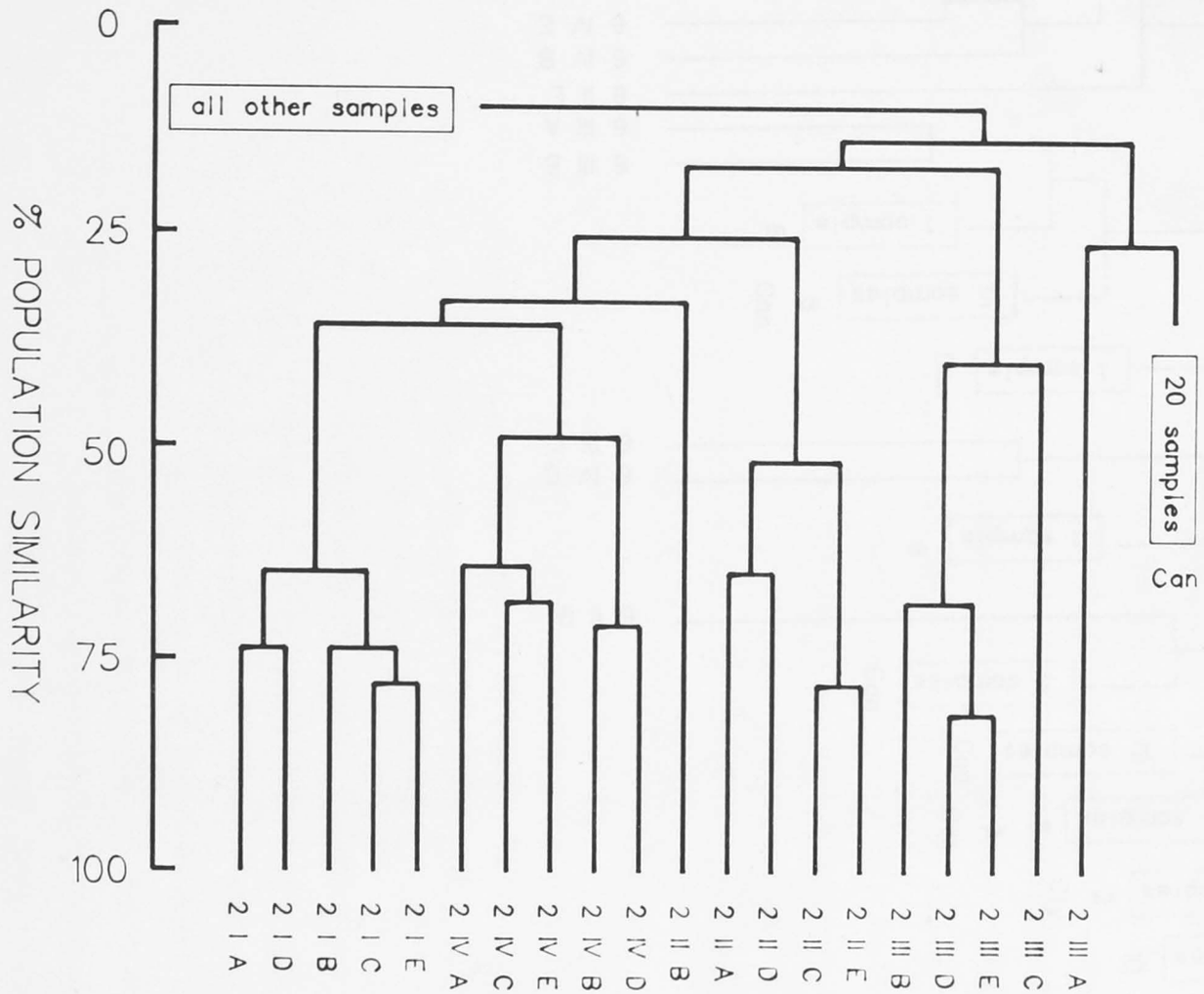
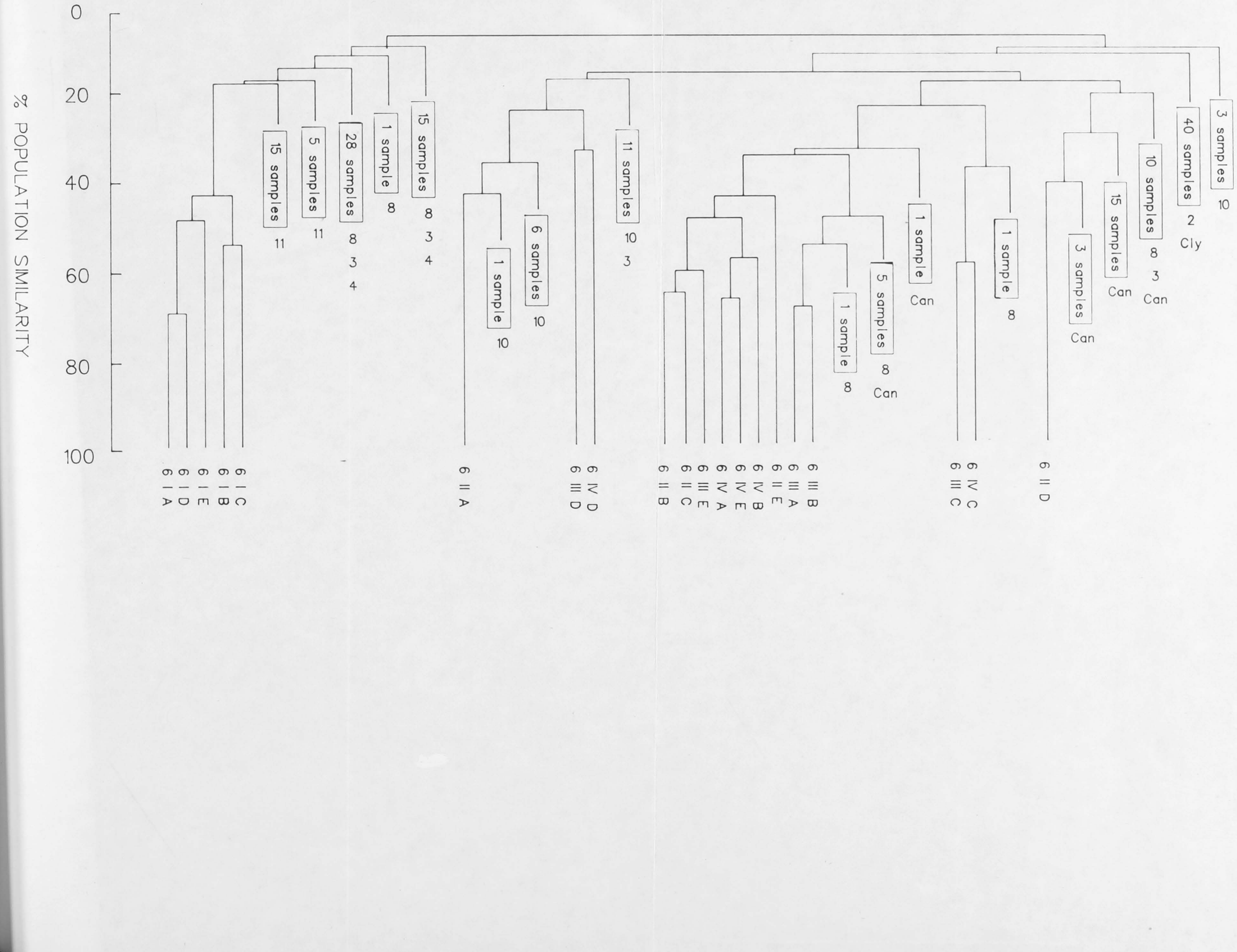


FIGURE 3.6 SIMPLIFIED DENDROGRAM SHOWING RELATIONSHIPS AMONG SAMPLES FROM SITE 6



analysis which gives only a qualitative measure of the importance of the major pattern relative to any deviations from it. Other types of analyses are more suitable for quantifying the importance of pattern. They are considered elsewhere (sections 3.2 and 3.3).

Whatever the absolute importance, the presence of this pattern indicates that deterministic processes operating on about the medium scale of sampling are an important determinant of population characteristics. The grain size characteristics of the sediment and the availability of oxygen and fine detritus in the sediment seem likely to be important factors behind the deterministic processes. The sites which were most distinguished by these factors, site 2 and the Clyde River, also had the most distinct population characteristics. Any relationships among the other sites were obscured by the complexity of the patterns and inconsistencies in the dendrogram. The importance of different environmental factors in determining population characteristics is investigated in more detail using other methods (section 3.2 and Chapter 4).

The inconsistencies in the medium scale pattern are probably caused by processes affecting the populations on the small scale. There are three possibilities as to the nature of the small scale variation. Cluster analysis cannot definitively distinguish between them, but stochastic processes appear most likely to be involved. The configuration of the actual dendrogram (Figure 3.3) is somewhat similar to the pattern produced by small scale stochastic processes (Figure 3.2a). Geographically distant samples were often more similar than neighbours and the individual samples grouped together at very different levels of similarity. The second possibility, small scale deterministic processes cannot be ruled out however, because it too produces formal similarities in distant samples (Figure 3.1a). Superimposing a small scale pattern over the medium scale pattern may also produce grouping of samples at very different levels of similarity. The third possible origin of the inconsistencies in the major pattern is due to the properties of cluster

analysis itself. Cluster analysis is very sensitive to population characteristics which fall into discrete groups, however it can be misleading when populations form gradients: very similar patterns can give very different dendrograms (Figure 3.7). However, it seems unlikely that the individual samples from different and geographically discrete sites formed an equidistantly spaced gradient. To verify this statement and clarify the less important processes, the population characteristics of the samples are examined another way in the next section.

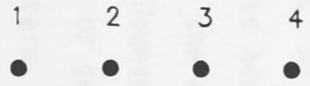
3.2 *FAUNAL GRADIENTS*

3.2.1 **Introduction**

Unlike cluster analysis, Principal Co-ordinate Analysis can be rather inefficient at identifying discrete groups and strong clusters of samples with similar population characteristics. However, Principal Co-ordinate Analysis is very useful when there is a more complex pattern in the data, particularly from one or more gradients. Principal Co-ordinate Analysis is also very useful in identifying and evaluating the effects of several different factors on population characteristics. It allows the effects of different factors to be separated onto different co-ordinates to clarify relationships which may not be apparent when the combined effects of many different factors are presented together on a single dendrogram. In addition, Principal Co-ordinate Analysis gives an indica tion as to the importance of any patterns identified according to how much of the total variation in population characteristics is attributable to each pattern (Chapter 2).

If one factor is of overwhelming importance, a single principal co-ordinate would be expected to account for most of the variation in population characteristics among the samples. The remaining co-ordinates would account for only minor variations from the major pattern. However, if several factors are all important determinants of population characteristics, then several principal co-ordinates would be required to

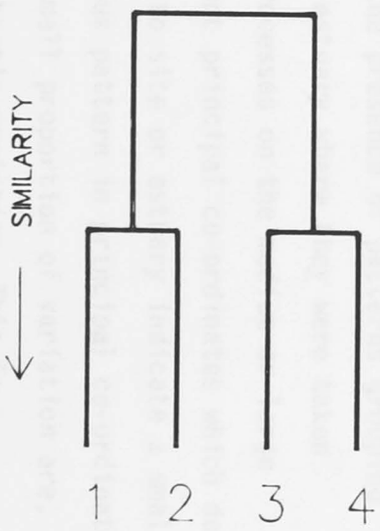
FIGURE 3.7 CLUSTER ANALYSIS AND EQUIDISTANT POINTS

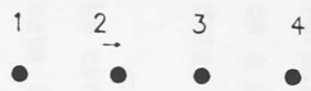


points equally spaced

points 2 & 3 dissimilar

2 major groups

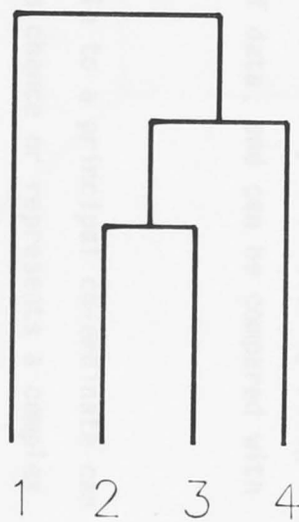


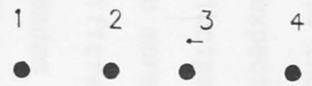


point 2 moved slightly right

points 2 & 3 most similar

point 1 most dissimilar

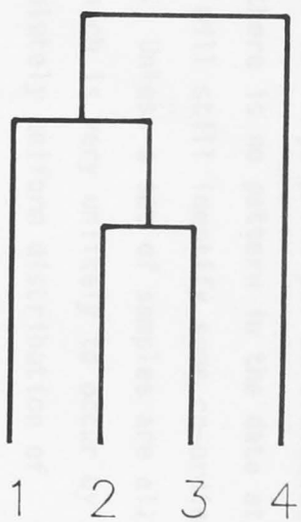




point 3 moved slightly left

points 2 & 3 most similar

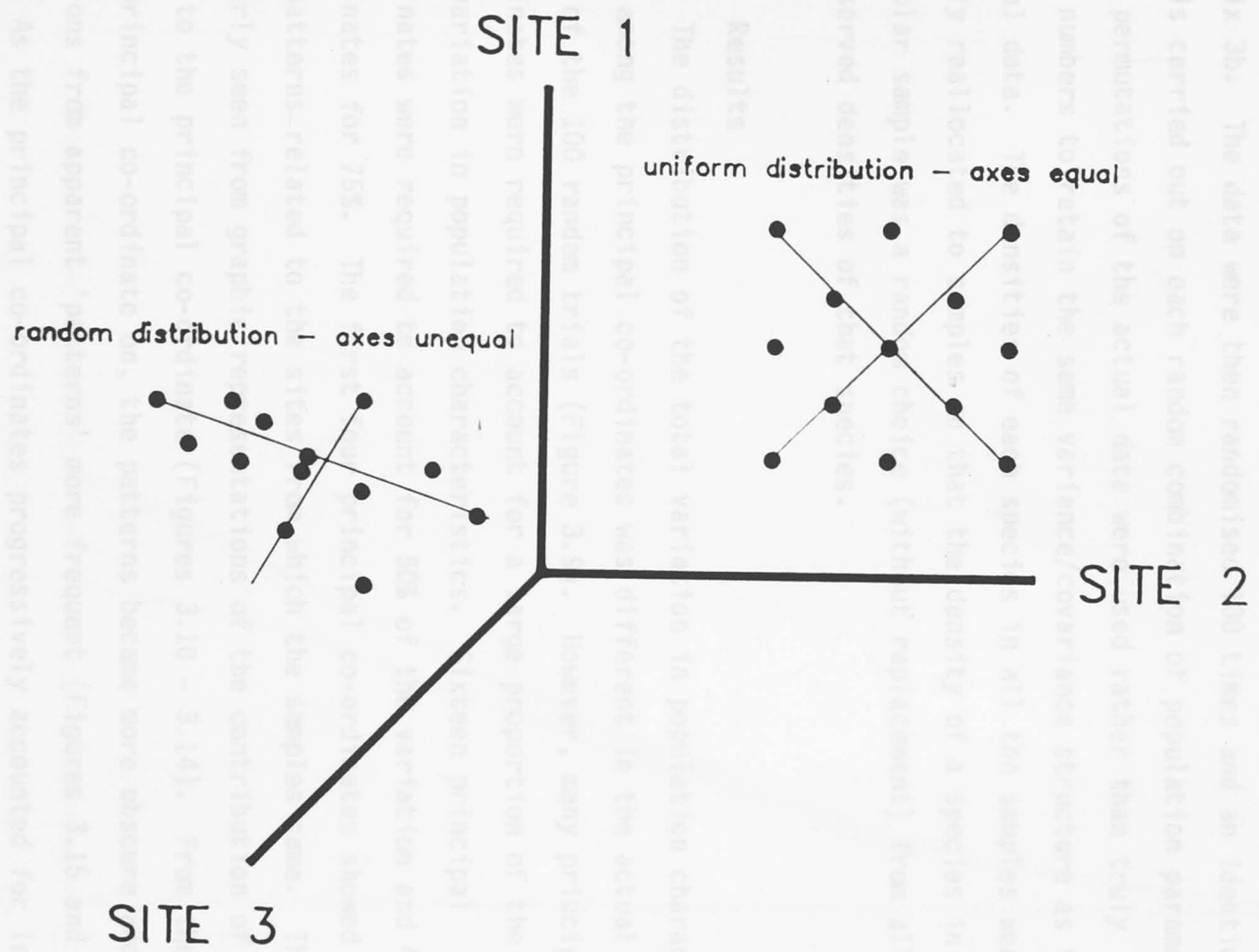
point 4 most dissimilar



account for any large portion of the population variability. If no major factors are involved (despite the pattern identified by cluster analysis in the previous section), then no large principal co-ordinates would be expected. However, even if there is no pattern in the data at all, a Principal Co-ordinate analysis will still identify some co-ordinates to be more important than others. Unless a set of samples are all equally different from one another, which is very unlikely to occur by chance, random variations from an absolutely uniform distribution of points will result in some principal co-ordinates accounting for more variation than others (Figure 3.8). Patterns generated in this way by random data are distinguishable from genuine patterns by the distribution the variance accounted for by each principal co-ordinate. The distributions characteristic of random data are easily estimated by doing the analysis on a number of random sets of data, and can be compared with the real data.

The contribution of each sample to a principal co-ordinate can also indicate if the pattern is due to chance or represents a complex pattern involving a number of principal co-ordinates which do not account individually for large portions of the total population variability. Strong patterns according to the site, time or estuary from which the samples came are also unlikely to be generated by random variation. As in cluster analysis, the presence of patterns grouping the samples according to the site or estuary where they were taken indicates the action of ecological processes on the medium or large scales. However, patterns in important principal co-ordinates which do not order or group samples according to site or estuary indicate a small scale pattern. The lack of any obvious pattern in principal co-ordinates which account for only a relatively small proportion of variation are, however, likely to indicate only stochastic variation. This is especially so when no samples contribute very much to the variation represented by a co-ordinate.

FIGURE 3.8 PRINCIPLE CO-ORDINATES OF UNIFORM AND RANDOM POINTS



3.2.2 Method

A Principal Co-ordinate Analysis of the population characteristics of all the samples was carried out as described in Chapter 2 and Appendix 3b. The data were then randomised 100 times and an identical analysis carried out on each random combination of population parameters. Random permutations of the actual data were used rather than truly random numbers to retain the same variance/covariance structure as the original data. The densities of each species in all the samples were randomly reallocated to samples so that the density of a species in any particular sample was a random choice (without replacement) from all the observed densities of that species.

3.2.3 Results

The distribution of the total variation in population characteristics among the principal co-ordinates was different in the actual data to any of the 100 random trials (Figure 3.9). However, many principal co-ordinates were required to account for a large proportion of the total variation in population characteristics. Sixteen principal co-ordinates were required to account for 50% of the variation and 48 co-ordinates for 75%. The first four principal co-ordinates showed clear patterns related to the sites from which the samples came. This is clearly seen from graphic representations of the contribution of each sample to the principal co-ordinate (Figures 3.10 - 3.14). From the fifth principal co-ordinate on, the patterns became more obscure and deviations from apparent 'patterns' more frequent (Figures 3.15 and 3.16). As the principal co-ordinates progressively accounted for less of the total variation, the contributions of the individual samples also became more uniformly low; no samples made outstanding or important contributions to these co-ordinates (Figure 3.16). This indicates that there were no important patterns in the least important co-ordinates (Appendix 3b).

FIGURE 3.9 PRINCIPAL CO-ORDINATES FROM ACTUAL AND RANDOM DATA

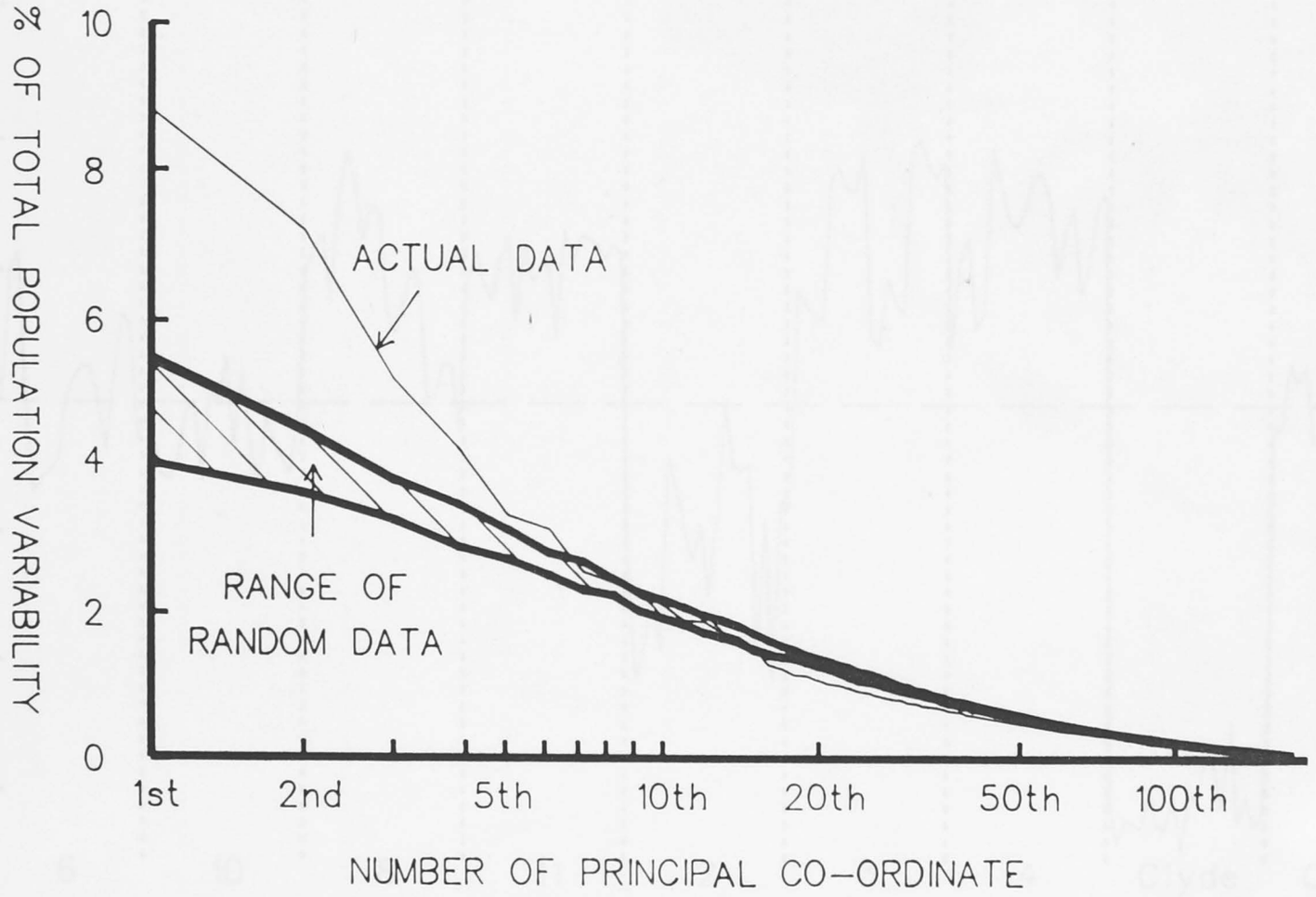


FIGURE 3.10 VALUES OF SAMPLES ON FIRST PRINCIPAL CO-ORDINATE

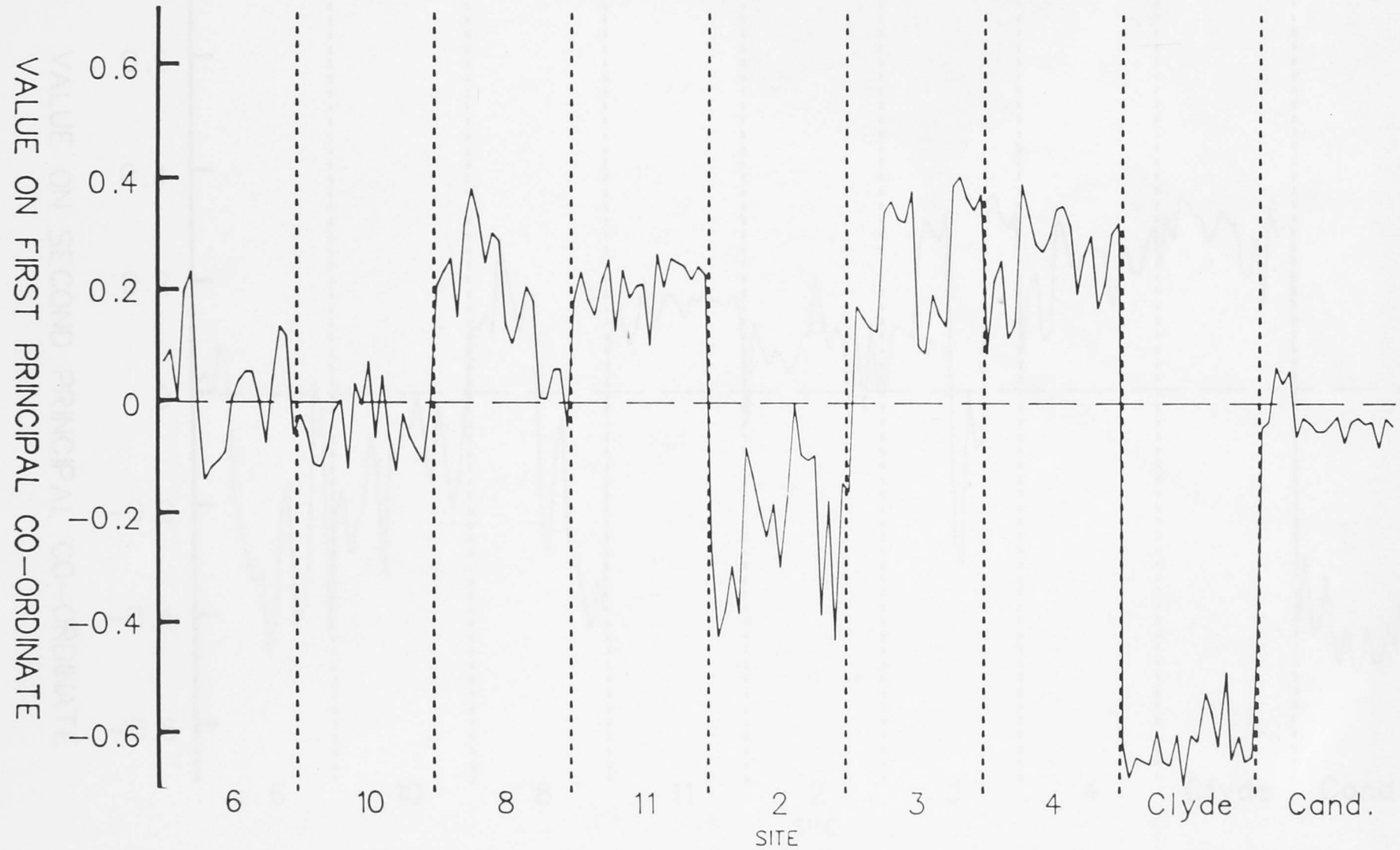


FIGURE 3.11 VALUES OF SAMPLES ON SECOND PRINCIPAL CO-ORDINATE

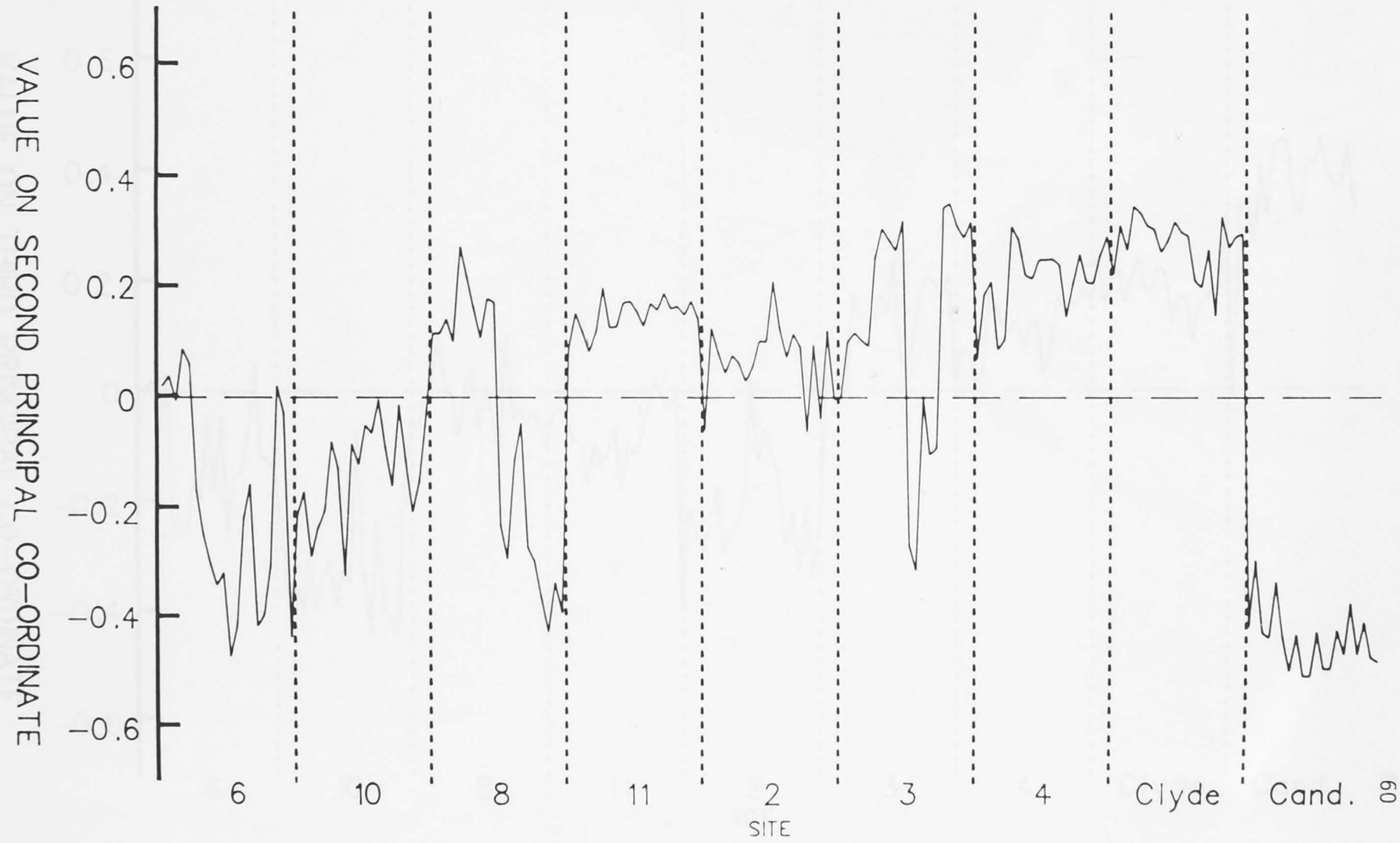


FIGURE 3.12 VALUES OF SAMPLES ON THIRD PRINCIPAL CO-ORDINATE

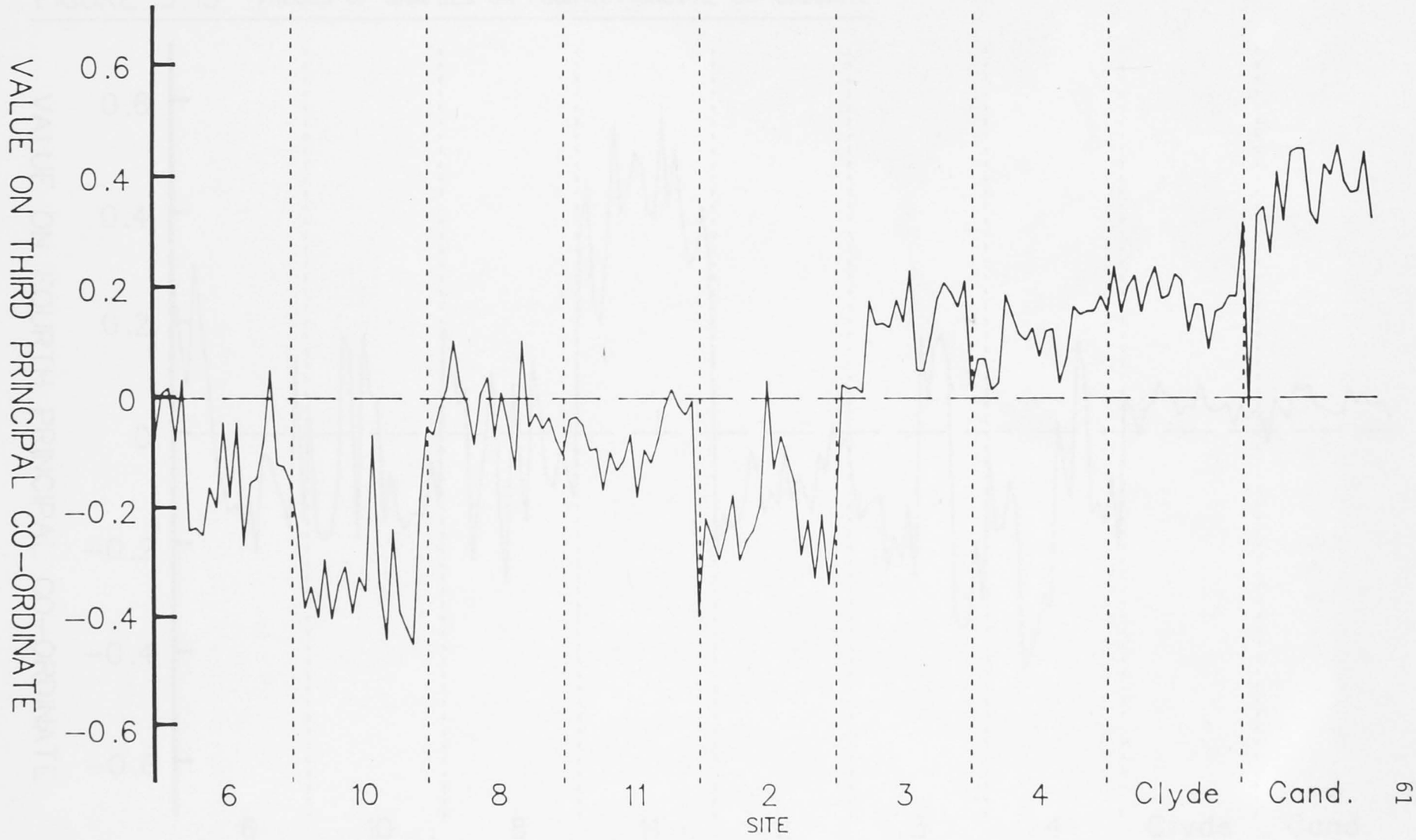


FIGURE 3.13 VALUES OF SAMPLES ON FOURTH PRINCIPAL CO-ORDINATE

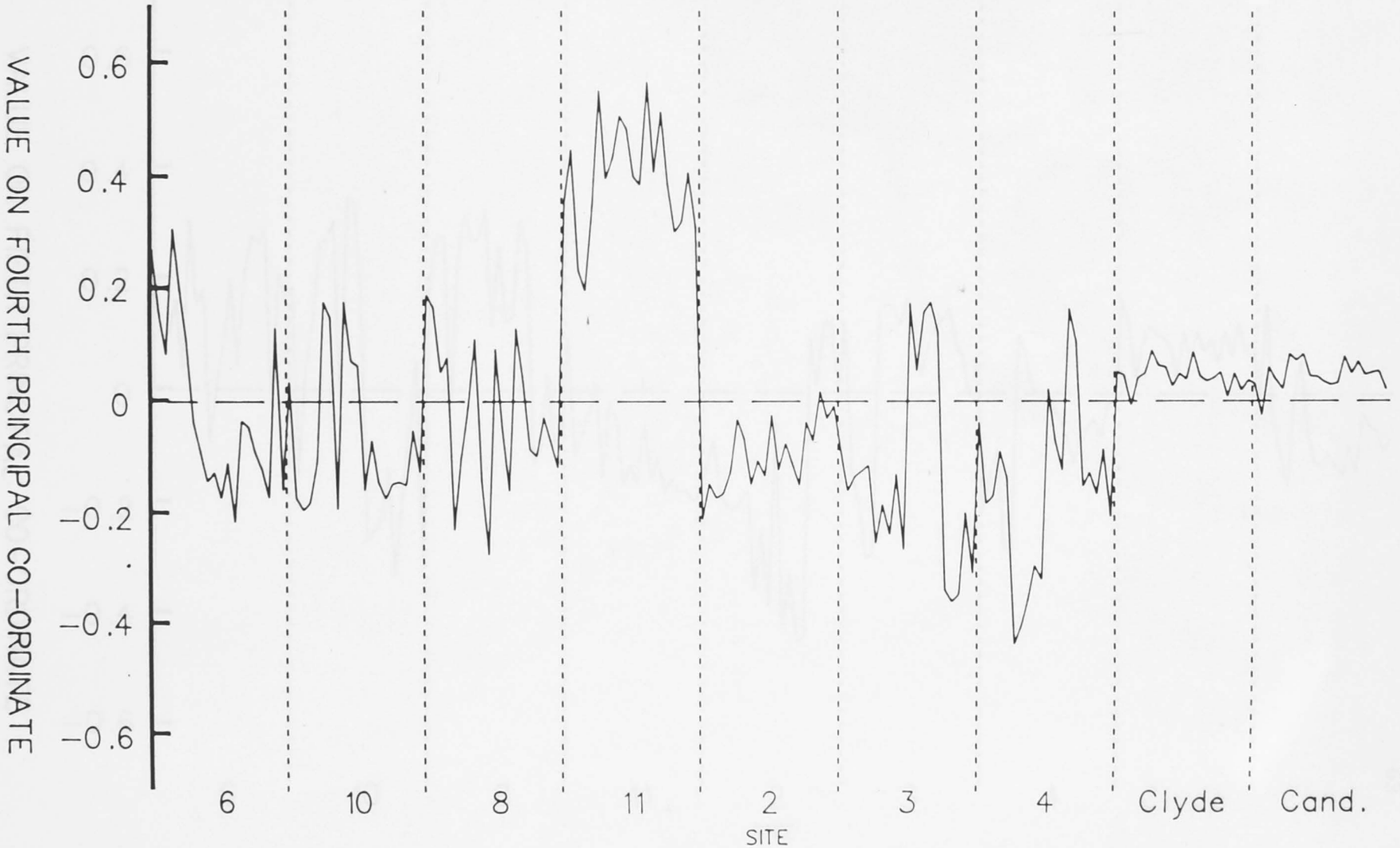


FIGURE 3.14 VALUES OF SAMPLES ON FIFTH PRINCIPAL CO-ORDINATE

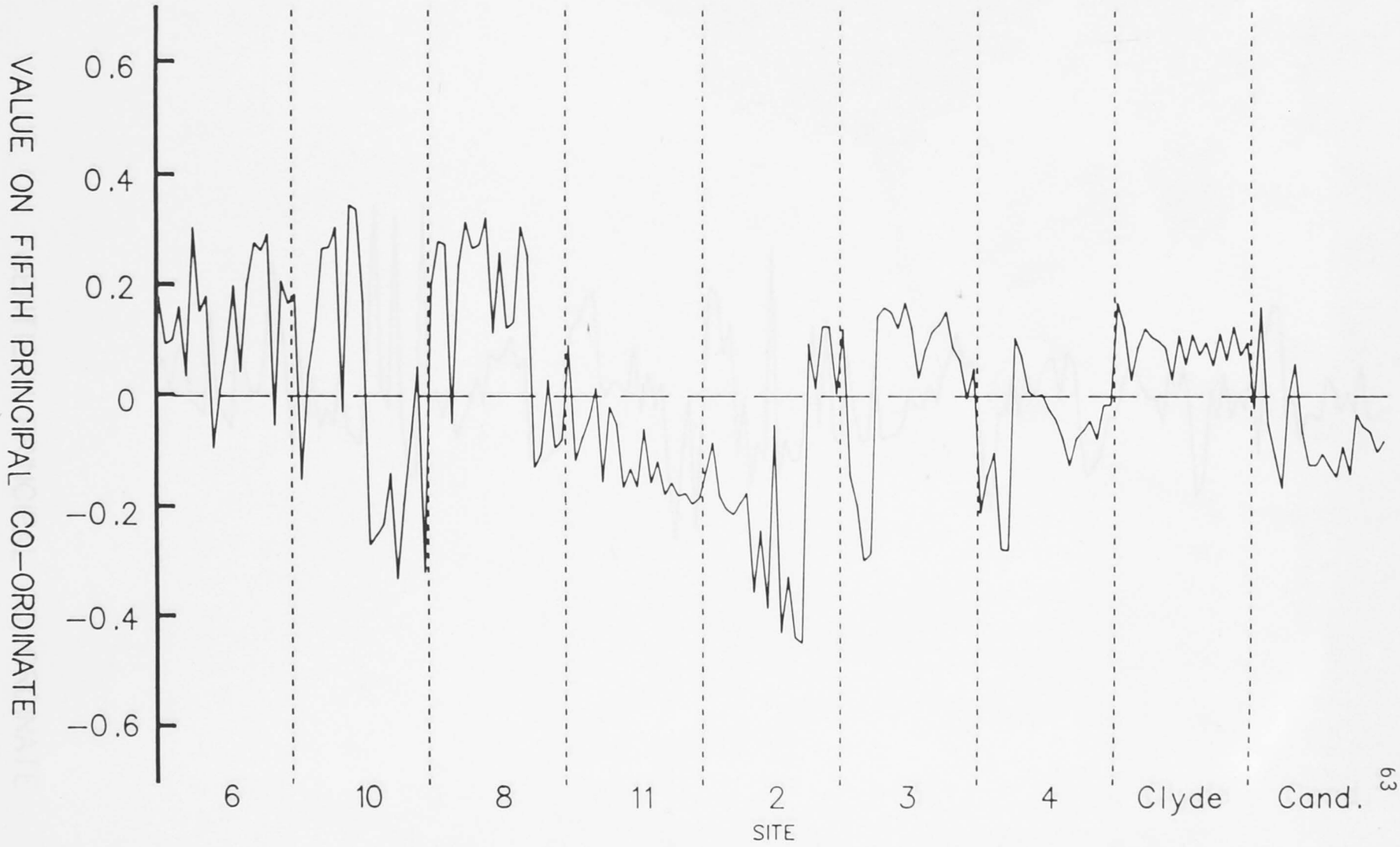


FIGURE 3.15 VALUES OF SAMPLES ON TWENTIETH PRINCIPAL CO-ORDINATE

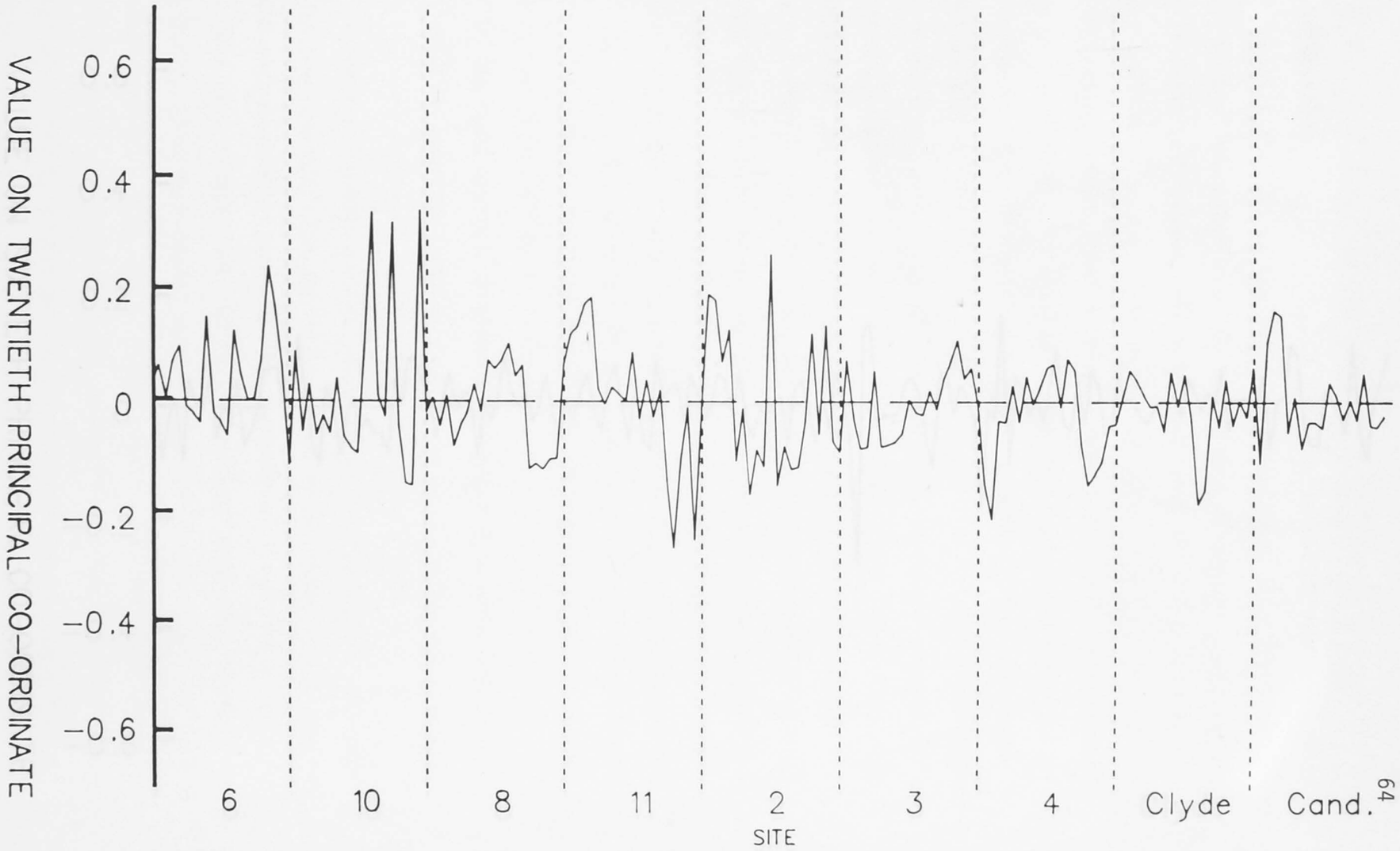
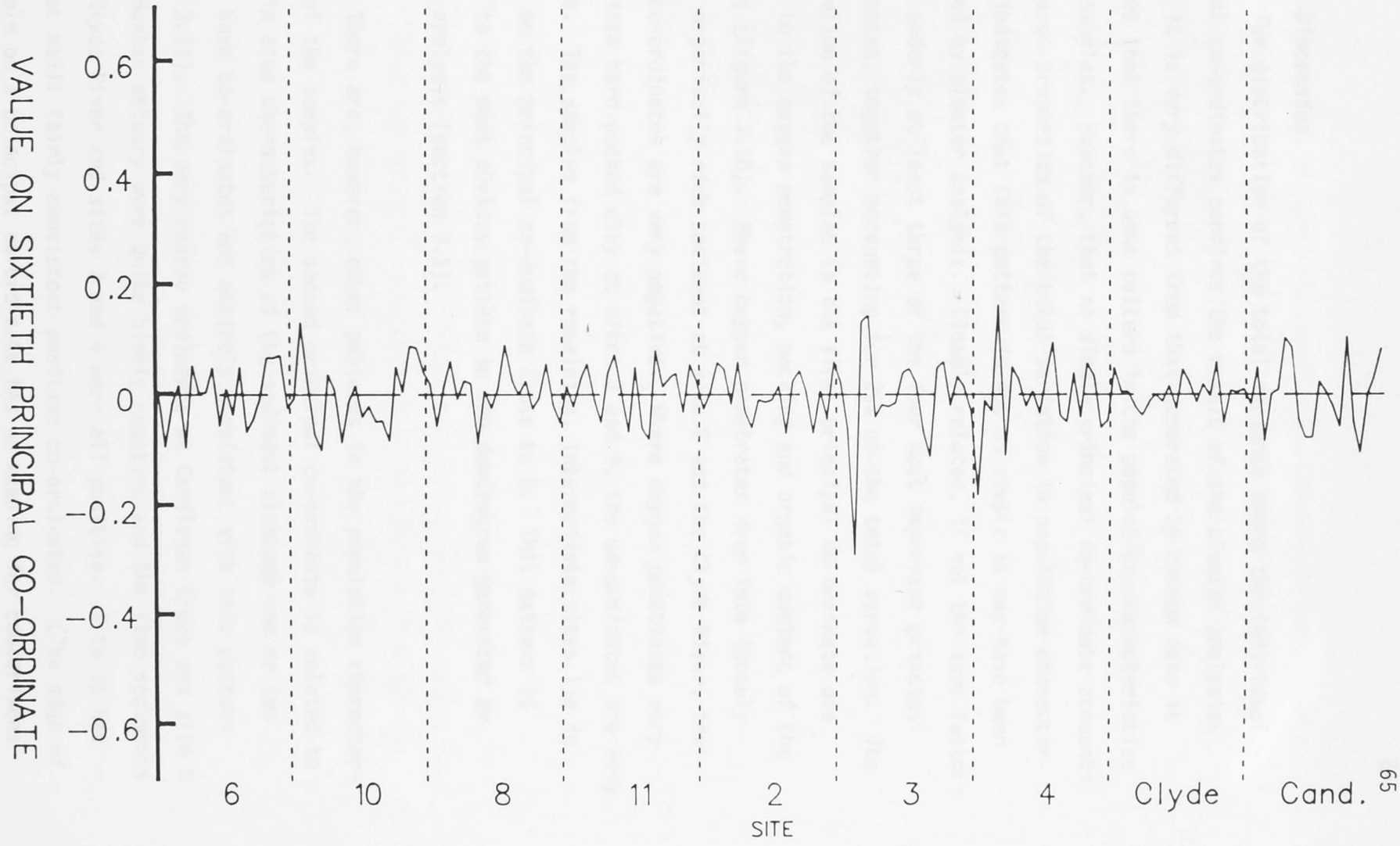


FIGURE 3.16 VALUES OF SAMPLES ON SIXTIETH PRINCIPAL CO-ORDINATE



3.2.4 Discussion

The distribution of the total variance among the individual principal co-ordinates confirms the result of the cluster analysis. Because it is very different from that generated by random data it indicates that there is some pattern in the population characteristics of the samples. However, that no single principal co-ordinate accounts for a large proportion of the total variation in population characteristics indicates that this pattern is not as simple as may have been suggested by cluster analysis. Closely related, if not the same factors seem to underly at least three of the four most important principal co-ordinates, together accounting for 25% of the total variation. The contribution of the samples to the first principal co-ordinate are related to the oxygen penetration, packing and organic content of the sediment (Figure 3.10). Where oxygen penetrates deep into loosely packed, organically rich sediment at site 2 and the Clyde River, the sample co-ordinates are very negative. Where oxygen penetrates very poorly into hard packed clay at sites 3 and 4, the co-ordinates are very positive. The samples from the remaining, intermediate sites lie in between on the principal co-ordinate close to 0. This pattern is similar to the most obvious pattern in the dendrogram generated by cluster analysis (section 3.1).

There are, however, other patterns in the population characteristics of the samples. The second principal co-ordinate is related to the grain size characteristics of the sediment although one or two samples have co-ordinates not entirely consistent with this pattern (Figure 3.11). The very coarse sediments at Candlagan Creek and site 6 in the Hunter estuary were quite highly negative and the fine sediments of the Clyde River and sites 3 and 4 were all positive. Site 11 had lower but still fairly consistent positive co-ordinates. (The sign of the sample on a principal co-ordinate has no meaning for comparisons between different co-ordinates.) The third co-ordinate seems to indicate some effect of the largest scale, contrasting sites 2 and 10 to the

Clyde and Candlagan estuaries (Figure 3.12). The fourth co-ordinate contrasted site 11 to sites 3 and 4 (Figure 3.13). All these sites have hard, clayey sediments, however, at site 11 the surface water drains very well during low tide leaving a dry, bare surface. By contrast, at sites 3 and 4 water lies almost permanently on the surface, which is covered by extensive algal mats. Although these patterns do not account for an overwhelming proportion of the total variation in population characteristics, they do indicate that deterministic processes are important on both medium and large scales.

At the other end of the scale, the smallest principal co-ordinates, which show no patterns at all, represent stochastic elements. Although separately accounting for only very small proportions of the total population variability, these minor principal co-ordinates are very numerous and together account for quite a substantial portion of population variability. However, there is no clear demarcation between the obvious and unequivocal patterns in the first few co-ordinates and the lack of any patterns in the last ones, and the principal co-ordinates intermediate between these two extremes account for a substantial portion of the total variance. The importance of the apparent patterns in these intermediate principal co-ordinates is investigated in the next section, where the relative contributions of the different scales and processes are further discussed.

3.3 *A QUANTITATIVE ASSESSMENT OF THE ROLES OF DIFFERENT SCALES AND PROCESSES IN POPULATION VARIABILITY.*

3.3.1 Introduction and Method

The statistical methods used in the previous two sections identified some important patterns in population characteristics on the medium scale and to a lesser degree in patterns on the large scale. They also suggest an important stochastic element in population characteristics. However, the relative contribution of the different processes and scales were difficult to quantify because of uncertainty in the

demarcation between the two processes. A better evaluation of the relative importance of the different processes and scales is not possible from the raw data on species abundances because of their unusual statistical distribution (Appendix 1). However, the values of each sample on a principal co-ordinate approximates a normal distribution with zero mean which is suitable for the powerful Analysis of Variance. An Analysis of Variance of the sample values for each principal co-ordinates will determine if there is any statistically significant pattern according to the site or time at which the sample was taken, or both. If there is a pattern according to site, or site and time, then medium or large scale processes are implicated. If there are no statistically significant patterns according to site or time in a co-ordinate then small scale changes are implicated.

Whether the statistically significant effects of site represented a deterministic pattern or stochastic variation was assessed qualitatively according to how well the patterns in the co-ordinates paralleled simple patterns in environmental factors among the sites. On the small scale, the distinction between deterministic and stochastic processes is based on the amount of variance accounted for by the co-ordinates. The co-ordinates accounting for most variance represent the most important patterns in population characteristics. As co-ordinates account for progressively less variation, they are less likely to show any pattern and more likely to show only stochastic variation. Hence, if a co-ordinate has a statistically significant pattern according to site or time, then it is very likely that all the co-ordinates which account for larger proportions of the variation also represent patterns in population characteristics. Therefore, all co-ordinates which are more important than the last co-ordinate in which the effects of site or time are statistically significant should represent patterns. If any of these more important co-ordinates has no significant pattern according to site or time then the pattern must be on the small scale and deterministic processes are implicated. However, a co-ordinate with no effect

site or time probably represents stochastic variation if it accounts for only a small proportion of the total variance and there are no statistically significant patterns in any less important co-ordinates. Such co-ordinates are very unlikely to represent any patterns in population characteristics, and therefore indicate stochastic variation.

The allocation of principal co-ordinates to the effects of any particular scale, however, depends on the level of statistical significance at which effects of site or time are recognised. For this reason, the results obtained using the above criteria were compared for two levels of significance - α=0.05 and α=0.001. The latter is a much more stringent condition for ascribing any pattern to the effects of site or time at which the samples were taken and consequently an easier criterion for allocating co-ordinates to small scale effects. Finally, the percentages of the total variation accounted for by the principal co-ordinates were summed according to the scale and population process which were primarily represented on each co-ordinate.

3.3.2 Results

The Analysis of Variance of the sample values on each co-ordinate, and the summary of the scale and process represented, are presented in Table 3.1. The total influence of the different scales and processes is shown in Figure 3.17. The level of probability at which the various processes and scales were deemed to be statistically significant had very little effect on the main results (Table 3.1).

The site at which the samples were taken was the most important influence on population characteristics, accounting for about 50% of the total variation. Much of the influence of the site at which a sample was taken on population characteristics was independent of the time at which the sample was taken - 30% of the total population variability (Figure 3.17). This portion of the population variation also includes many of the most important principal co-ordinates which represent

TABLE 3.1 Patterns in Principal Co-ordinates

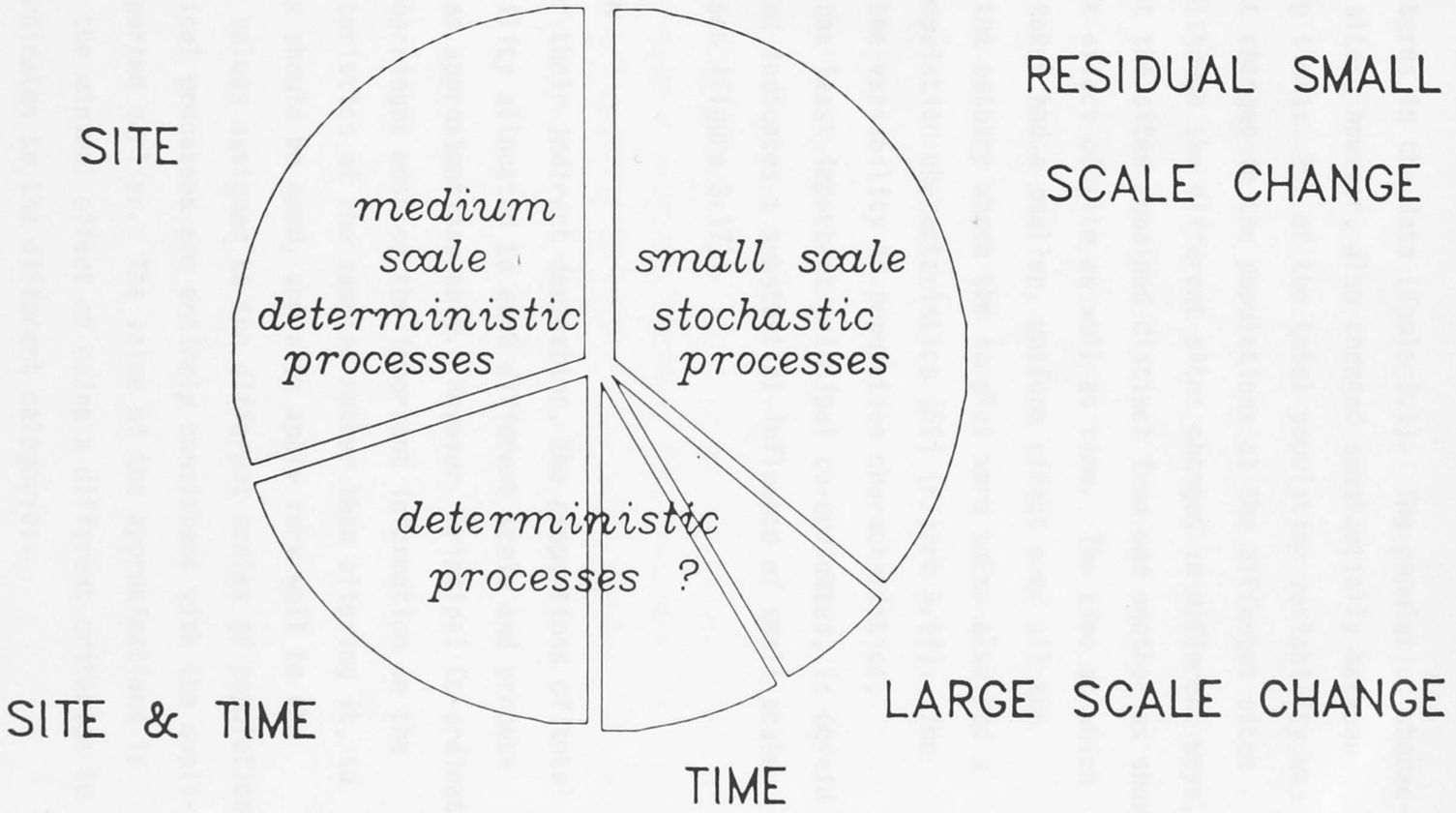
Principal Co-ordinate	% Variance	F-Ratio Site	F-Ratio Time	F-Ratio Site & Time
1	8.85	481.7 *	5.8 **	8.1 *
2	7.19	191.7 *	15.6 *	18.1 *
3	5.16	179.5 *	3.2 **	4.8 *
4	4.24	68.0 *	10.8 *	11.1 *
5	3.33	26.7 *	6.1 *	8.1 *
6	3.15	36.0 *	29.2 *	10.3 *
7	2.56	28.3 *	7.0 *	17.2 *
8	2.42	22.8 *	7.7 *	7.4 *
9	2.32	16.0 *	10.5 *	14.9 *
10	2.10	12.1 *	29.8 *	10.9 *
11	1.89	9.1 *	19.3 *	12.6 *
12	1.87	20.1 *	7.5 *	9.1 *
13	1.73	30.1 *	0.4	9.2 *
14	1.66	4.5 *	11.0 *	7.3 *
15	1.53	13.4 *	4.8 **	8.0 *
16	1.28	8.1 *	25.9 *	8.8 *
17	1.23	2.0	7.9 *	3.2 *
18	1.14	9.5 *	3.6 **	8.6 *
19	1.13	2.6 **	4.0 **	5.8 *
20	1.07	2.7 **	2.6	3.2 *
21	1.02	1.3	2.3	3.3 *
22	0.99	1.3	3.0 **	1.9 **
23	0.96	2.5 **	3.2 **	4.5 *
24	0.91	2.5 **	1.6	4.2 *
25	0.90	1.0	4.6 **	3.0 *
26	0.86	0.7	6.1 *	2.4 **
27	0.83	0.6	1.4	2.7 *
28	0.81	0.2	1.5	1.9 **
29	0.80	0.4	2.5	2.3 **
30	0.76	0.2	1.0	2.2 **
		df=8, 44	df=3, 108	df=24, 108

* $P < 0.001$

** $P < 0.05$

Underlined numbers indicate the most important influence(s) on each Principal Co-ordinate (as summarised in Fig. 3.15)

FIGURE 3.17 PROPORTION OF TOTAL POPULATION VARIATION ACCOUNTED FOR BY DIFFERENT SCALES AND PROCESSES



the strongest patterns in the data (Table 3.1). The population characteristics of the sites, however, also changed substantially between different sampling times: 20% of the total population variability was due to independent changes in the populations at the different sites (Figure 3.17). Although the different sites changed in different ways, the populations at the sites remained distinct from one another as shown by the significant effect of site as well as time. The time at which the samples were taken had a smaller, uniform effect over all the samples (8%) and the estuary where the samples were taken also had a small effect on population characteristics (5%) (Figure 3.17). The remaining 35% of the variability in population characteristics, representing all the least important principal co-ordinates, is devoid of any patterns and indicates a substantial influence of small scale stochastic processes (Figure 3.17).

3.3.3 Discussion

Because of their indirect derivation, the proportions of total population variability allocated to each different scale and process must be regarded as approximations only. However, Principal Co-ordinate Analysis merely rearranges most of the important information on the population characteristics of the samples rather than altering it, so the approximations should be good, and also apply very well to the actual data. The values assigned to the different scales of population change and ecological processes are entirely consistent with the qualitative results reported earlier. The value of the approximations is also supported by the minimal effect of using a different criterion to allocate the co-ordinates to the different categories.

The method for deciding if there was likely to be a pattern in the principal co-ordinates presented no problems in practice. All the co-ordinates which had no statistically significant pattern according to site, time or both formed a block of the least important co-ordinates (Table 3.1). This is a very important result because it indicates that

there were no patterns in this block and no small scale patterns which were strong enough to override the patterns according to site or time. Full discussion of these results is delayed until Chapter 6, because more detailed examination of some of the components of population changes are investigated more fully in the succeeding chapters. The general discussion will also consider further the nature of the considerable changes in population characteristics over time, especially the different temporal changes at the various sites. These changes could be seasonal or may represent stochastic changes within the populations at each site. If they do represent stochastic changes, the changes are either of a nature unique to each site or of insufficient magnitude to change the essential character of the populations. Of the alternatives, the latter may be marginally more probable because most of the patterns which comprise the site and time portion of the total variance are relatively unimportant. Without data from more than one year, however, it is impossible to tell whether this is the origin of the temporal population variation or whether it represents seasonal change.

CHAPTER 4

POPULATION PROCESSES ON THE SMALL SCALE

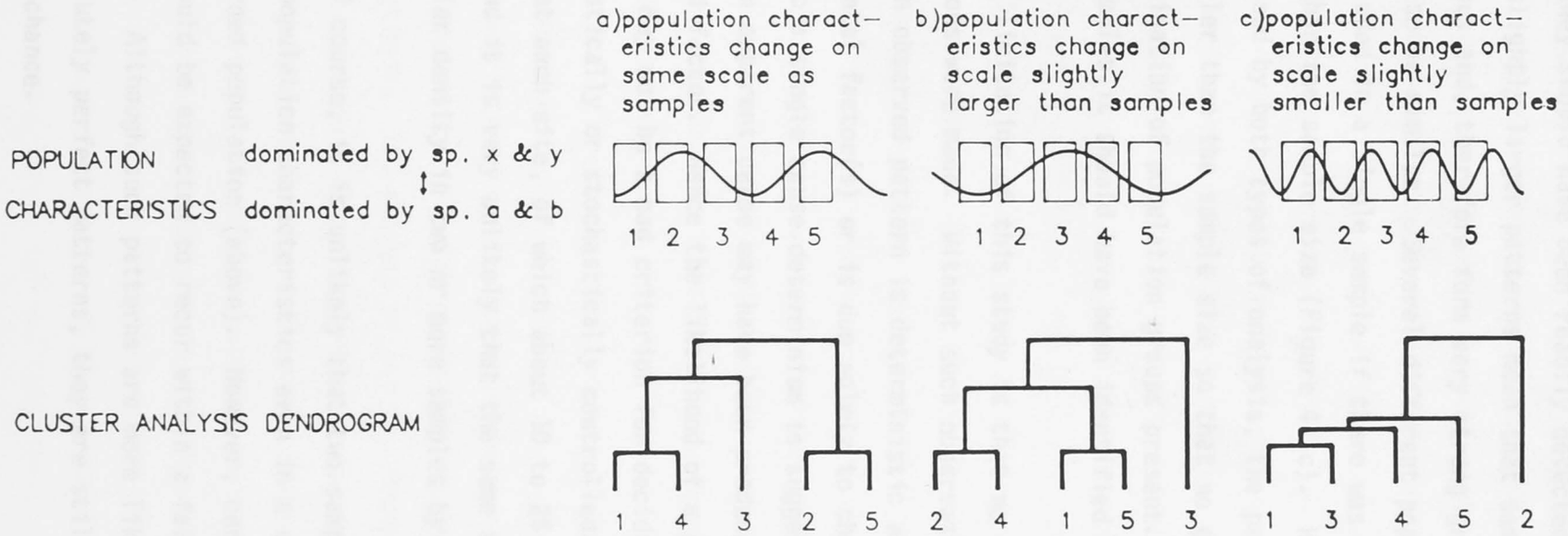
4.1 *SMALL SCALE PATTERNS IN POPULATION CHARACTERISTICS IN THE FIELD*

4.1.1 Introduction

The Principal Co-ordinate and cluster analyses reported in Chapter 3 found no major patterns in the population characteristics of the samples on the smallest scale. However, although unlikely for reasons discussed in sections 3.2 and 3.3, it is possible that patterns among the individual samples may have been overlooked. In analysing the data from all the different sites together, any patterns on a small scale may have been dominated by more important patterns among the different sites. The interaction of simultaneous changes to the populations on two different scales in this way may also have produced some of the variability which could not be attributed to any pattern on any scale. The possibility that there are small scale patterns in population characteristics which have been obscured by larger scale changes was considered here by examining each site separately. Any strong groupings of the samples should thus be apparent, free from the larger scale patterns.

A perfect pattern could not be expected, even if the population characteristics were perfectly determined in small patches (Figure 4.1). Some samples may have covered part of several different patches or fallen at different levels on a gradient (Figure 4.1a). Others may have been located in areas intermediate between two different faunal types. Either of these possibilities would weaken the appearance of any pattern observed in a cluster analysis by interposing samples of intermediate population characteristics between major clusters. However, Principal Co-ordinate Analysis should still recognise some such pattern in a fairly important co-ordinate. Patterns in population characteristics on a scale slightly larger than the sample size are not as serious (Figure

FIGURE 4.1 PATTERNS PRODUCED BY CHANGES ON SCALES CLOSE TO THE SAMPLE SIZE



PRINCIPAL CO-ORDINATE ANALYSIS (value of samples)		a)	b)	c)
	axis 1	samples 1 & 4 high samples 2 & 5 high opposite sign	samples 1 & 5 high samples 2 & 4 medium	samples 1,2,4 & 5 high
	axis 2		site 3 high samples 2 & 4 medium	site 3 high

4.1b). They should have been readily detected by either analysis because slightly larger patterns mean that samples are more likely to be homogeneous and, therefore form very strong groups. Adjacent samples should also be similar. Several different population groups may have been included in a single sample if there was a pattern at a scale smaller than the sample size (Figure 4.1c). However, for such patterns to be missed by both types of analysis, the pattern would have to be much smaller than the sample size so that no groups of samples had the same combination of population groups present. If there is any pattern in the samples it should have been identified by these analyses.

A limitation of this study is that no small scale environmental observations were made. Without such observations it is difficult to tell if an observed pattern is deterministic and can be related to some environmental factor(s) or is due solely to chance. If a pattern can be related to a single cause determinism is suggested. However, a pattern without an apparent cause may have been produced by an unexpected and unmeasured factor. Hence the likelihood of a pattern occurring solely by chance may not be a bad criterion for deciding if the populations are deterministically or stochastically controlled. About 50 species occurred at each site, of which about 10 to 25 were present in any one sample, and it is very unlikely that the same species would occur at a very similar density in two or more samples by chance alone.

Of course, it is unlikely that two samples would have exactly the same population characteristics even in a very strongly determined and patterned population (above). However, certain combinations of species could be expected to recur within a fairly small range of variation. Although such patterns are more likely to occur by chance than absolutely perfect patterns, they are still unlikely to occur solely by chance.

4.1.2 Method

Cluster and Principal Co-ordinate Analyses were carried out as described in sections 3.1 and 3.2 and Appendix 3, except that the 20 samples from each site were analysed separately.

4.1.3 Results

The complete results for each site are in Appendix 5, however, the results from site 2 and Candlagan Creek, which are presented here, are representative. These are also the sites investigated experimentally (section 4.2). There were some patterns in the dendrograms produced by cluster analysis, however, few groups of samples were very strong (Figures 4.2 and 4.3). The levels of similarity at which samples fused were also very variable at both sites. In the Principal Co-ordinate Analysis, many co-ordinates were required to account for any substantial proportion of the total population variability (Tables 4.1 and 4.2). Five out of 20 principal co-ordinates were required to account for half the total variance and nine co-ordinates for 75% of the variance at both sites. The most important patterns were according to the time that samples were taken.

4.1.4 Discussion

These results agree with the conclusions from Chapter 3 and add weight to the earlier results by confirming the efficiency of the initial methods. The absence of any important patterns (apart from that due to the different times of sampling) again indicates that stochastic processes were predominant on the small scale. Neither analysis detected any pattern and few adjacent samples were very similar indicating that slightly larger patterns were not involved. This result probably applies to all scales close to that of the samples. Of course, little can be said about scales very different from the samples, however, more might be said after dispersal has been investigated in the next section. Movement is important when small patterns are considered.

FIGURE 4.2 RELATIONSHIPS AMONG SAMPLES FROM SITE 2: CLUSTER ANALYSIS

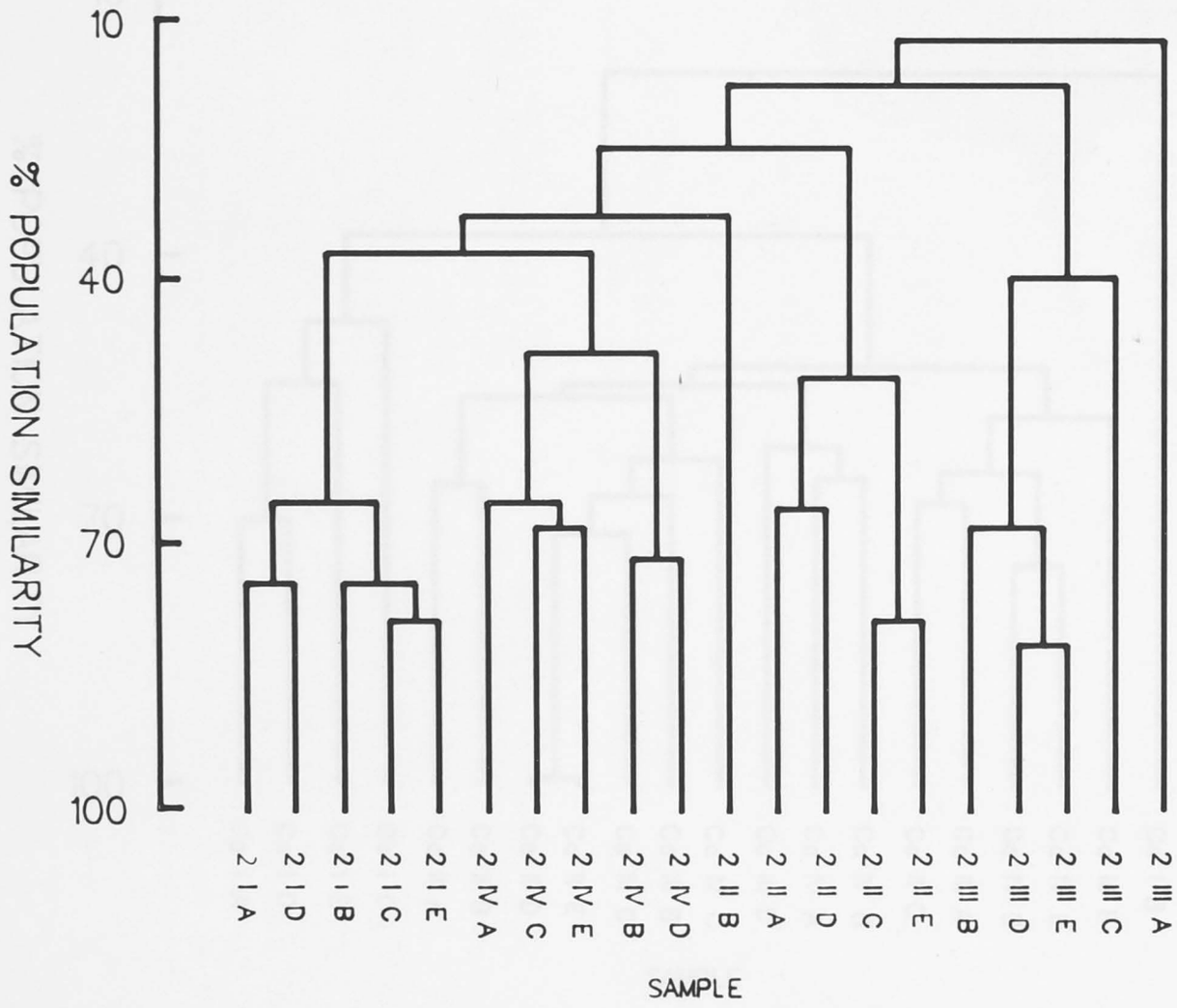


FIGURE 4.3 RELATIONSHIPS AMONG SAMPLES FROM CANDLAGAN CREEK: CLUSTER ANALYSIS

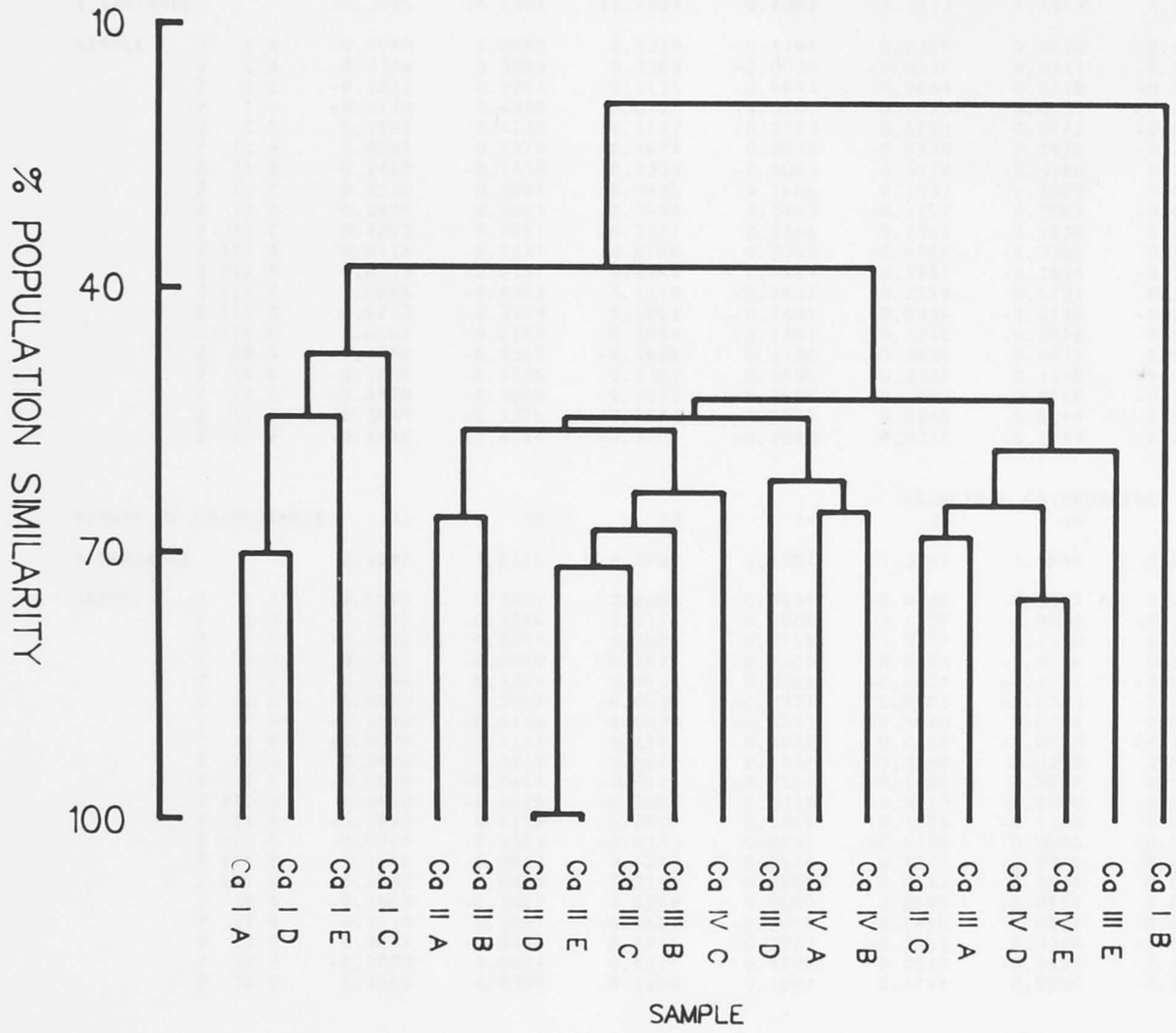


TABLE 4.1 Values of samples on principal co-ordinate axes - site 2

			PRINCIPAL CO-ORDINATE									
NUMBER OF CO-ORDINATE			1	2	3	4	5	6	7	8	9	10
% VARIANCE			22.3995	14.7501	11.7827	9.4082	7.3812	5.4962	4.0226	3.6094	3.2148	2.9896
SAMPLE	2	I A	-0.1940	0.2898	0.0379	-0.4284	0.0150	-0.0033	0.0979	-0.3177	0.3489	0.1519
	2	I B	-0.2378	0.3099	0.3362	-0.0038	-0.0230	0.0331	-0.0997	0.0447	0.0479	-0.0713
	2	I C	-0.1231	0.3954	0.3135	-0.0894	0.0684	0.0730	-0.0984	0.0253	-0.2474	-0.0898
	2	I D	-0.2124	0.4048	0.0722	-0.3585	0.0093	0.0435	-0.0306	-0.0729	0.0021	-0.0002
	2	I E	-0.1865	0.4130	0.1742	-0.1743	0.0791	0.0772	-0.0007	0.0969	-0.2640	0.0216
	2	II A	0.0904	0.2274	-0.4624	0.2832	-0.4839	0.1918	-0.2907	-0.1308	0.0079	0.0092
	2	II B	-0.2460	-0.1438	-0.3239	-0.4063	-0.3574	-0.3160	0.0280	0.3739	0.0334	0.0768
	2	II C	0.3130	0.2897	-0.3425	0.1606	0.1831	-0.1092	0.3062	0.0020	0.0018	-0.0089
	2	II D	0.0846	0.3001	-0.3594	0.3453	-0.1452	0.1003	-0.0234	0.0823	0.0023	0.0620
	2	II E	0.4062	0.2857	-0.2077	0.2366	0.2351	-0.1039	0.2424	0.0322	0.0441	-0.0456
	2	III A	0.0116	-0.2127	0.5766	0.3359	-0.4766	-0.3301	0.2069	-0.2188	-0.1215	0.0445
	2	III B	0.6019	-0.0117	0.0394	0.0414	0.2451	-0.1918	-0.1108	-0.0341	-0.0110	-0.1336
	2	III C	0.5065	-0.4391	0.1170	-0.2437	-0.2159	0.5731	0.2985	0.0642	-0.0167	-0.0802
	2	III D	0.6723	-0.3159	0.1052	-0.1409	0.0419	-0.0745	-0.2253	0.0242	0.0232	0.0816
	2	III E	0.6662	-0.2704	0.1094	-0.1361	0.1240	-0.0878	-0.2271	-0.0058	0.0274	0.0781
	2	IV A	-0.4486	-0.4367	-0.1926	0.1190	0.2425	0.0837	0.0009	-0.1426	-0.1377	0.3433
	2	IV B	-0.3885	-0.1505	0.2382	0.2905	0.2327	0.1148	-0.0036	0.2396	0.0537	0.2148
	2	IV C	-0.4820	-0.3860	-0.2181	0.0698	0.1799	0.0768	-0.1048	-0.1830	-0.0250	-0.2590
	2	IV D	-0.3849	-0.1375	0.3073	0.3075	0.0140	0.0294	-0.0505	0.1708	0.3431	-0.1831
	2	IV E	-0.4488	-0.4114	-0.3205	-0.2083	0.0317	-0.1799	0.0777	-0.0503	-0.1122	-0.2123

			PRINCIPAL CO-ORDINATE								
NUMBER OF CO-ORDINATE			11	12	13	14	15	16	17	18	19
% VARIANCE			2.1047	1.8575	1.7702	1.6387	1.3797	1.3546	1.2224	1.1334	0.0000
SAMPLE	2	I A	-0.0018	0.0622	0.0260	0.0639	-0.0748	0.0194	0.0301	-0.0908	0.0933
	2	I B	-0.1582	-0.2266	0.0179	0.0006	0.1117	0.0301	-0.2665	0.0171	0.0848
	2	I C	-0.1455	0.0044	0.1006	0.0758	0.0217	0.1122	0.1602	-0.1852	-0.0839
	2	I D	0.1467	-0.0899	-0.1815	-0.1382	0.0473	-0.0346	0.0311	0.1175	-0.2174
	2	I E	0.1299	0.1764	0.0831	0.0166	-0.0624	-0.1357	-0.0002	0.1386	0.1652
	2	II A	-0.0862	0.2057	-0.0536	-0.0327	0.0963	-0.0043	-0.0278	-0.0036	-0.0001
	2	II B	-0.1592	-0.0149	0.0333	-0.0741	-0.0840	0.0126	0.0276	0.0012	-0.0020
	2	II C	-0.0028	0.1137	0.1905	0.0610	-0.0120	-0.0153	-0.1673	-0.0035	-0.1674
	2	II D	0.2220	-0.2819	-0.0079	0.1416	-0.1568	0.0230	0.0566	-0.0235	0.0347
	2	II E	-0.0596	-0.0464	-0.0571	-0.2059	0.1688	0.0484	0.1423	0.0129	0.1337
	2	III A	0.0450	-0.0029	-0.0093	-0.0415	-0.0413	0.0066	0.0066	0.0147	-0.0098
	2	III B	-0.1995	0.0299	-0.2518	0.1055	-0.1776	-0.1131	-0.0144	-0.0000	0.0015
	2	III C	-0.0574	-0.0183	-0.0383	0.0147	-0.0184	0.0005	-0.0057	0.0055	0.0017
	2	III D	0.1616	-0.0644	0.1243	-0.0946	0.1005	-0.1976	-0.0137	-0.1537	-0.0072
	2	III E	0.0739	0.0416	0.0740	0.0580	0.0092	0.2624	0.0032	0.1643	0.0025
	2	IV A	-0.1988	-0.1022	0.0252	0.0689	0.0695	-0.0797	0.0529	0.0808	-0.0275
	2	IV B	0.1119	0.1607	-0.1682	-0.0846	-0.0490	0.0887	-0.0873	-0.1250	-0.0102
	2	IV C	0.0086	-0.0316	0.1215	-0.2263	-0.1913	0.0368	-0.0200	-0.0025	0.0128
	2	IV D	-0.0073	0.0534	0.0915	0.1109	0.0643	-0.0953	0.1266	0.0956	-0.0514
	2	IV E	0.1765	0.0309	-0.1202	0.1804	0.1784	0.0350	-0.0341	-0.0605	0.0469

TABLE 4.2 Values of samples on principal co-ordinate axes - Candlagan Creek

			PRINCIPAL CO-ORDINATE									
NUMBER OF CO-ORDINATE			1	2	3	4	5	6	7	8	9	10
% VARIANCE			17.2833	11.9910	11.0754	8.7188	7.0245	5.7713	5.6102	5.3067	4.7382	3.6488
SAMPLE	CAN	I A	0.4744	-0.0682	-0.0036	-0.0060	0.0051	-0.3295	-0.2648	0.2317	-0.1799	0.0442
	CAN	I B	0.2631	-0.3924	-0.8163	-0.0842	0.2589	0.0833	0.1321	0.0087	-0.0716	-0.0114
	CAN	I C	0.4314	0.0692	-0.0496	0.0362	-0.4634	0.2055	0.2430	0.2235	0.1641	-0.0408
	CAN	I D	0.5449	0.0539	0.2089	0.0828	0.1099	-0.1387	-0.2021	0.0354	0.0273	-0.0739
	CAN	I E	0.6091	0.0347	0.2266	0.1935	0.2064	0.2489	0.0240	-0.3142	0.2067	0.1629
	CAN	II A	-0.0434	0.2117	-0.0995	-0.0609	-0.2144	-0.3502	0.2504	-0.2676	-0.0224	0.0770
	CAN	II B	-0.0192	0.2413	-0.1651	-0.2212	-0.0406	-0.2448	-0.0548	-0.0077	0.3237	-0.1748
	CAN	II C	-0.2731	-0.1976	-0.1234	0.1935	-0.1685	-0.0582	-0.2747	-0.1266	0.0543	0.0466
	CAN	II D	-0.1074	-0.4101	0.1670	-0.1880	-0.2299	0.0743	-0.0833	-0.0701	-0.0433	0.0320
	CAN	II E	-0.1074	-0.4101	0.1670	-0.1880	-0.2299	0.0743	-0.0833	-0.0701	-0.0433	0.0320
	CAN	III A	-0.3189	-0.1945	-0.0703	0.3105	0.0356	0.0874	-0.0967	0.0886	0.0659	0.0175
	CAN	III B	-0.0273	0.0140	0.1687	-0.4369	0.0816	0.1527	0.1121	-0.0202	-0.0937	-0.2554
	CAN	III C	-0.1454	-0.0832	0.2893	-0.1325	0.1993	0.0211	0.0944	0.1121	-0.1551	0.0952
	CAN	III D	-0.2621	0.2362	-0.0770	0.1322	0.0231	0.1988	-0.2479	-0.0925	0.0224	-0.2740
	CAN	III E	0.0245	-0.0608	0.2154	0.2608	0.1319	-0.1296	0.2355	-0.1725	-0.2417	-0.2100
	CAN	IV A	-0.1406	0.4776	-0.2379	0.1604	-0.1670	0.1123	-0.0267	-0.1244	-0.2929	0.1217
	CAN	IV B	-0.0111	0.4426	0.0109	-0.1006	0.0639	0.1803	-0.0645	0.2842	-0.1114	0.0895
	CAN	IV C	-0.2503	0.1506	0.0031	-0.3767	0.1806	-0.0255	-0.0427	-0.0857	0.1197	0.2619
	CAN	IV D	-0.2322	-0.1162	0.1300	0.2772	-0.0277	-0.0842	0.2363	0.2297	0.0548	0.0799
	CAN	IV E	-0.4092	0.0013	0.0559	0.1476	0.2451	-0.0786	0.1139	0.1378	0.2166	-0.0201

			PRINCIPAL CO-ORDINATE							
NUMBER OF CO-ORDINATE			11	12	13	14	15	16	17	18
% VARIANCE			3.2359	2.6961	2.3590	2.1656	1.8080	1.7446	1.3477	0.0000
SAMPLE	CAN	I A	-0.0681	-0.0451	0.1970	-0.0255	-0.1106	-0.1334	0.0258	0.0401
	CAN	I B	-0.0298	-0.0260	-0.0634	-0.0188	0.0314	0.0192	-0.0239	-0.0045
	CAN	I C	-0.1336	0.1501	-0.0063	0.0853	-0.0992	0.0139	0.0256	0.0156
	CAN	I D	0.0023	0.1440	-0.1428	0.1125	0.2382	0.1196	-0.1009	-0.0181
	CAN	I E	0.0621	-0.1352	0.0854	-0.0631	-0.0609	-0.0370	0.0008	-0.0006
	CAN	II A	0.0186	0.0893	0.0456	-0.1882	0.0196	0.0557	-0.1377	0.0856
	CAN	II B	0.2124	-0.1276	-0.1160	0.0259	-0.0817	-0.0626	0.0557	-0.1217
	CAN	II C	-0.0937	-0.0899	0.0668	0.0415	-0.0960	0.2822	0.0867	-0.0209
	CAN	II D	0.0471	-0.0735	-0.1033	-0.0061	0.0534	-0.0791	-0.0107	0.0480
	CAN	II E	0.0471	-0.0735	-0.1033	-0.0061	0.0534	-0.0791	-0.0107	0.0480
	CAN	III A	0.3190	0.3246	0.1118	-0.0622	-0.0041	-0.0498	0.0092	-0.0155
	CAN	III B	0.0741	-0.0235	0.3051	0.0441	0.0682	0.0947	0.0041	-0.0129
	CAN	III C	-0.0103	0.0457	-0.1166	0.0163	-0.2448	0.0645	-0.1817	-0.1300
	CAN	III D	-0.2720	0.0317	-0.0231	-0.1556	-0.0133	-0.1053	-0.1037	-0.0135
	CAN	III E	-0.0291	0.0601	-0.1296	0.0226	-0.0573	-0.0248	0.2220	0.0219
	CAN	IV A	0.0949	-0.0867	0.0237	0.2372	0.0474	-0.0776	-0.0433	-0.0507
	CAN	IV B	0.1198	-0.0933	-0.1314	-0.2004	0.0234	0.1065	0.1016	0.1083
	CAN	IV C	-0.2157	0.2160	0.0091	0.0543	0.0577	-0.0588	0.1480	-0.0315
	CAN	IV D	-0.1065	-0.1796	0.0745	-0.1007	0.1962	-0.0255	0.0151	-0.1636
	CAN	IV E	-0.0385	-0.1074	0.0168	0.1871	-0.0211	-0.0234	-0.0820	0.2160

It is also possible that sampling was insufficiently intense to detect a complex pattern in population characteristics. However, it is not possible to estimate the number of samples needed to detect a pattern without testing the statistical significance of population variation between different samples. To do this, one must evaluate the variability within samples, which requires a still smaller scale of sampling. It is also difficult to estimate the number of samples needed to detect a pattern without some notion as to the cause of the population pattern. The most prominent factors which are likely to cause a pattern in population characteristics on the small scale are mangrove leaves, roots and pneumatophores, pools of surface water, patches of algae and crab holes. Undoubtedly, there are also many other factors which may have influenced population characteristics (section 1.4.1a). Nevertheless, the most prominent factors were covered by at least several samples at each site and so groups of quite similar samples would be expected if any had a strong influence on population characteristics. That no patterns were detected is, of course, subject to the limitations of the sampling method and schedule (Chapters 2 and 6), but suggests that stochastic processes are important on the small scale. However, this hypothesis must be more tentative than if a positive pattern had been found. The small scale population processes are investigated further in the next section.

The importance of changes in population characteristics over time must be emphasised again, although nothing can be said about these changes without more than one years data. Temporal changes are discussed later in Chapter 6 in the light of all other results.

4.2 *EXPERIMENTAL SIMULATION OF FIELD PROCESSES*

4.2.1 Introduction

The statistical analyses of the field data all indicated that stochastic processes controlled population characteristics on the small scale. This analysis was not, however, totally unequivocal so an experiment was designed to test whether deterministic or stochastic processes were more important on the small scale. The different processes can be distinguished by following the fate of a known homogeneous population from a large area after being introduced into defaunated but otherwise intact sediment. If stochastic processes control the population characteristics then the initial homogeneous population should remain homogeneous in colonising the defaunated sediment. The populations in newly colonised areas should be random assortments of the original, introduced population. If the population characteristics are controlled by deterministic processes, however, there should be patterns in the distribution of animals. Dispersing animals should segregate into groups according to whatever factors are important. If taken from a large enough area, the initial population should include representatives of species from different small patches which should re-separate when allowed to disperse through relatively undisturbed sediment.

Greater understanding of how and why the particular processes operate can be gained from examining how the nematodes disperse. When stochastic processes operate, species typically occur unpredictably. One reason for this may be that all available habitat is not colonised well. However, if the population characteristics are determined strongly by some environmental factor, then efficient dispersal is expected to quickly colonise all available habitat. Many different patterns of dispersal are possible. Many individuals may disperse slowly or only a few disperse more quickly. Animals may disperse constantly or only when conditions deteriorate where they are. The potential for population increase may be low so that, even after suitable habitat has been found, the population builds up slowly or only certain stages of the life cycle may disperse.

Examining these aspects of disperal should give further insight into why the two different processes operate as they do in estuarine littoral nematode communities.

4.2.2 Method

A concentrated solution of the nematodes from the fine mud of site 2 in the Hunter estuary was introduced into a 5 cm radius circle in the centre of an experimental tray which contained a uniform layer of drained and defaunated sediment, also from site 2. After the inoculum had infiltrated into the mud, but before the tray was initially inundated, a set of samples was taken. One sample was taken at 5, 15 and 30 cm from the centre a little anti-clockwise of each of the 4 half-diagonals (see diagram under Table 4.4). Subsequent sets of samples were taken after 34 days (a little clockwise of the diagonals), 64 days (a little clockwise of the 30 day samples) and 93 days (a little anti-clockwise of the initial samples). Nematodes and mud from Candlagan Creek were used in a similar experiment. Both experiments ran from October to January.

4.2.3 Results

Statistical assessment of results was precluded by low animal densities in the peripheral samples and limited replication, but several clear results emerged for both types of mud. Despite considerable variation in the occurrence of each species throughout the experiment (Table 4.3), all species were largely confined to the inoculated area at the start (Table 4.3) and then dispersed outwards without directional bias (Table 4.4). Dispersal was generally slow but the rate varied somewhat between species (Figures 4.4 and 4.5), and a few individuals of *Spirinia* sp., *Theristus* sp., *Desmodora cazca* and *Diplolaimelloides* sp. (a generally uncommon species) appeared at the periphery of the tray before day 34. Adult females and occasional males of all species except *D. cazca* and *Sabatieria* sp. eventually colonised all the tray uniformly. Juveniles of *Spirinia* sp., *Theristus* sp., *Parodontophora* sp. and some less common species were also present throughout the trays.

TABLE 4.3 Dispersal of frequently occurring nematode species

Distance	DAY 0 5cm				15 cm				30 cm				DAY 34 5 cm				15 cm				30 cm			
Species																								
Hunter River Site 2 Mud																								
Desmodora cazca	93	71	51	89	1	-	-	-	-	-	-	-	49	59	27	67	17	5	9	5	-	-	1	-
Sabatieria sp	25	21	34	17	-	-	-	-	-	-	-	-	18	21	6	9	2	7	-	4	-	-	-	-
Spirinia sp	11	19	6	12	2	1	-	-	-	-	-	-	9	3	12	7	3	3	7	1	1	-	-	-
Tripyloides sp	5	2	17	6	-	-	-	-	-	-	-	-	1	4	1	6	2	3	-	-	-	-	-	-
Others	22	5	3	1	3	-	2	1	-	-	-	-	-	1	3	1	1	2	13	-	-	-	1	1
Candlagan Creek Mud																								
Spirinia sp	28	8	43	21	2	-	1	-	-	-	-	-	2	3	4	10	8	3	1	1	1	-	1	2
Theristus spp.	2	7	6	10	-	-	-	2	-	-	-	-	5	7	7	7	5	6	5	2	1	3	-	1
Gomphionema sp	3	6	7	6	-	-	-	-	-	-	-	-	8	1	3	-	2	-	2	-	-	-	-	-
Parodontophora sp	4	4	-	1	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	1	-	-
Ptycholaimellus sp	3	-	-	1	-	-	-	-	-	-	-	-	1	3	1	-	-	-	3	1	-	-	-	-
Others	8	2	3	2	-	1	-	-	-	-	-	-	3	6	2	-	1	8	3	3	1	2	-	-

Distance	DAY 64 5cm				15 cm				30 cm				DAY 93 5 cm				15 cm				30 cm			
Species																								
Hunter River Site 2 Mud																								
Desmodora cazca	2	2	3	3	2	3	1	-	2	3	2	-	1	2	2	2	1	2	2	2	1	1	-	1
Sabatieria sp	2	1	-	1	2	-	-	2	1	1	1	-	2	1	1	1	0	1	-	4	-	1	1	-
Spirinia sp	1	2	1	-	1	-	1	-	4	-	2	-	1	-	-	1	2	-	1	-	-	1	2	-
Tripyloides sp	4	-	2	-	2	-	-	1	-	2	-	7	1	-	1	-	-	-	-	1	2	-	-	2
Others	-	3	-	2	-	-	1	-	3	-	2	4	-	2	-	-	-	-	-	3	2	-	-	-
Candlagan Creek Mud																								
Spirinia sp	2	4	-	3	3	5	-	4	-	1	-	1	4	3	4	1	4	-	1	1	1	4	1	3
Theristus spp.	3	-	3	-	-	-	2	-	1	-	1	1	2	3	4	4	1	-	3	1	-	1	-	1
Gomphionema sp	-	2	3	1	-	-	3	1	-	2	-	3	1	1	-	1	1	-	-	1	1	1	-	3
Parodontophora sp	-	-	2	-	-	3	2	-	1	1	1	1	2	4	4	2	-	-	3	1	1	-	1	1
Ptycholaimellus sp	1	-	3	-	3	4	-	-	1	2	1	1	4	3	-	1	1	-	1	2	1	-	1	-
Others	-	-	-	-	3	-	7	1	3	-	-	1	1	4	-	1	3	2	1	1	-	1	7	1

TABLE 4.4 Gross Directional Movement

Position of Population Centre (Angle in degrees)*

Time	0	34	64	93
SPECIES				
Sites 2/8				
Desmodora cazca	23	34	90	0
Sabatieria sp.	-159	94	45	175
Spirinia sp.	87	-148	54	-167
Tripyloides sp.	-153	94	66	- 6
Candlagan Creek/Clyde River				
Spirinia sp.	-178	-135	65	75
Theristus spp.	-159	126	-90	-108
Gomphionema sp.	-135	56	-169	- 11
Parodontophora sp.	82	79	177	-103
Ptycholaimellus sp.	27	-135	-135	0

* Calculated by defining all samples according to the coordinate system shown below and then averaging the coordinates of all individuals of a species. Zero angle is the positive x-axis.

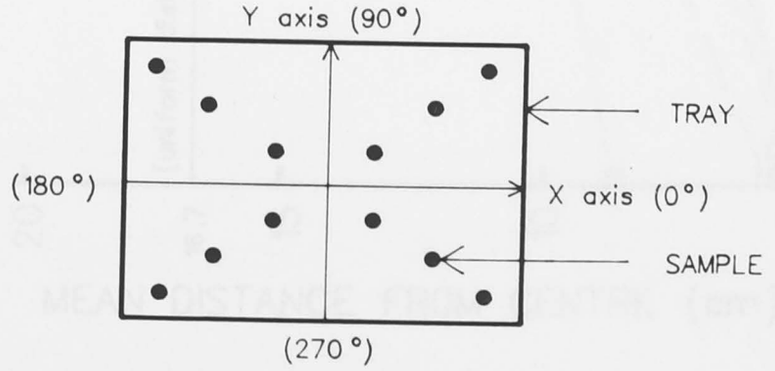


FIGURE 4.4 DISPERSAL OF ABUNDANT SPECIES IN MUD FROM SITE 2

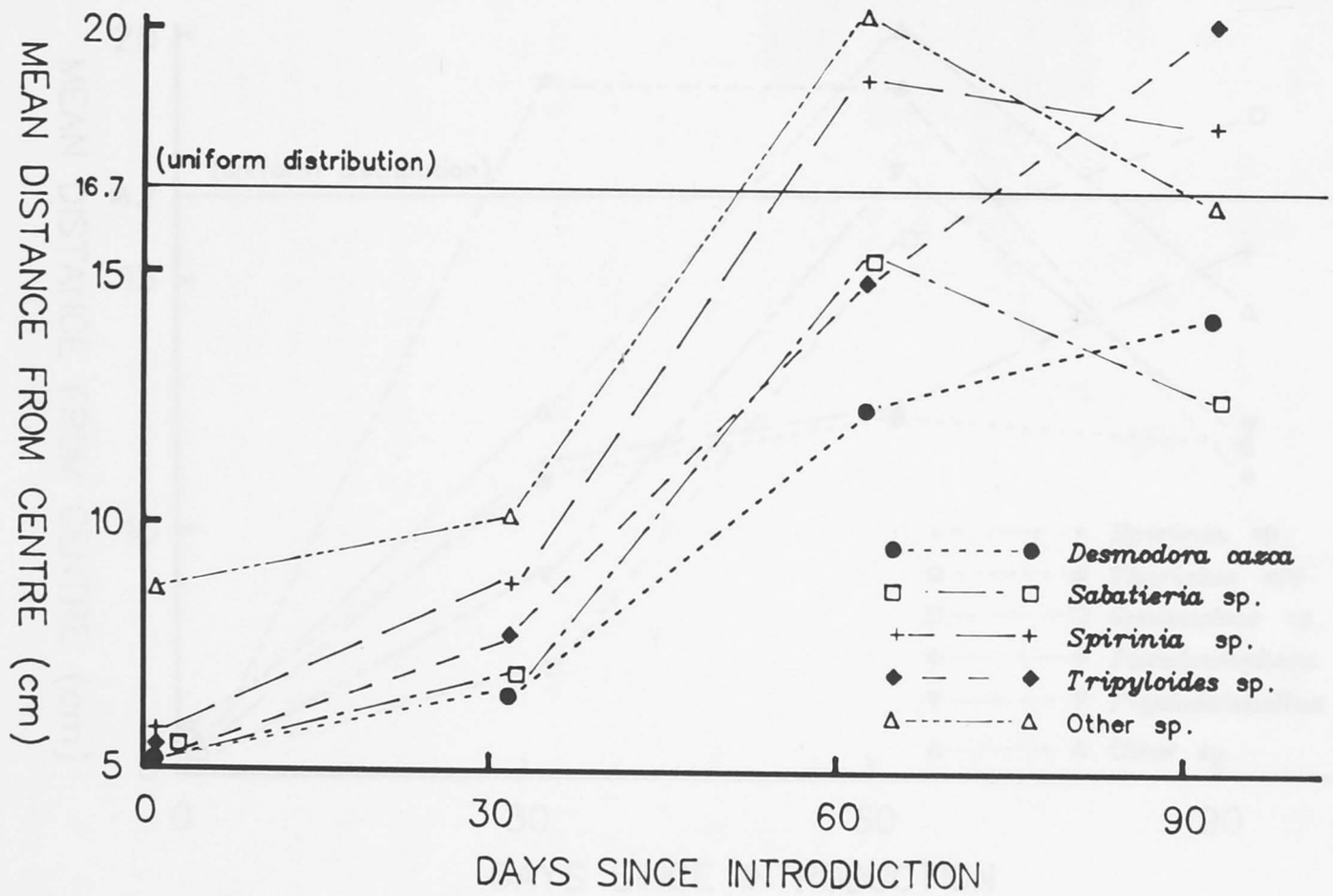
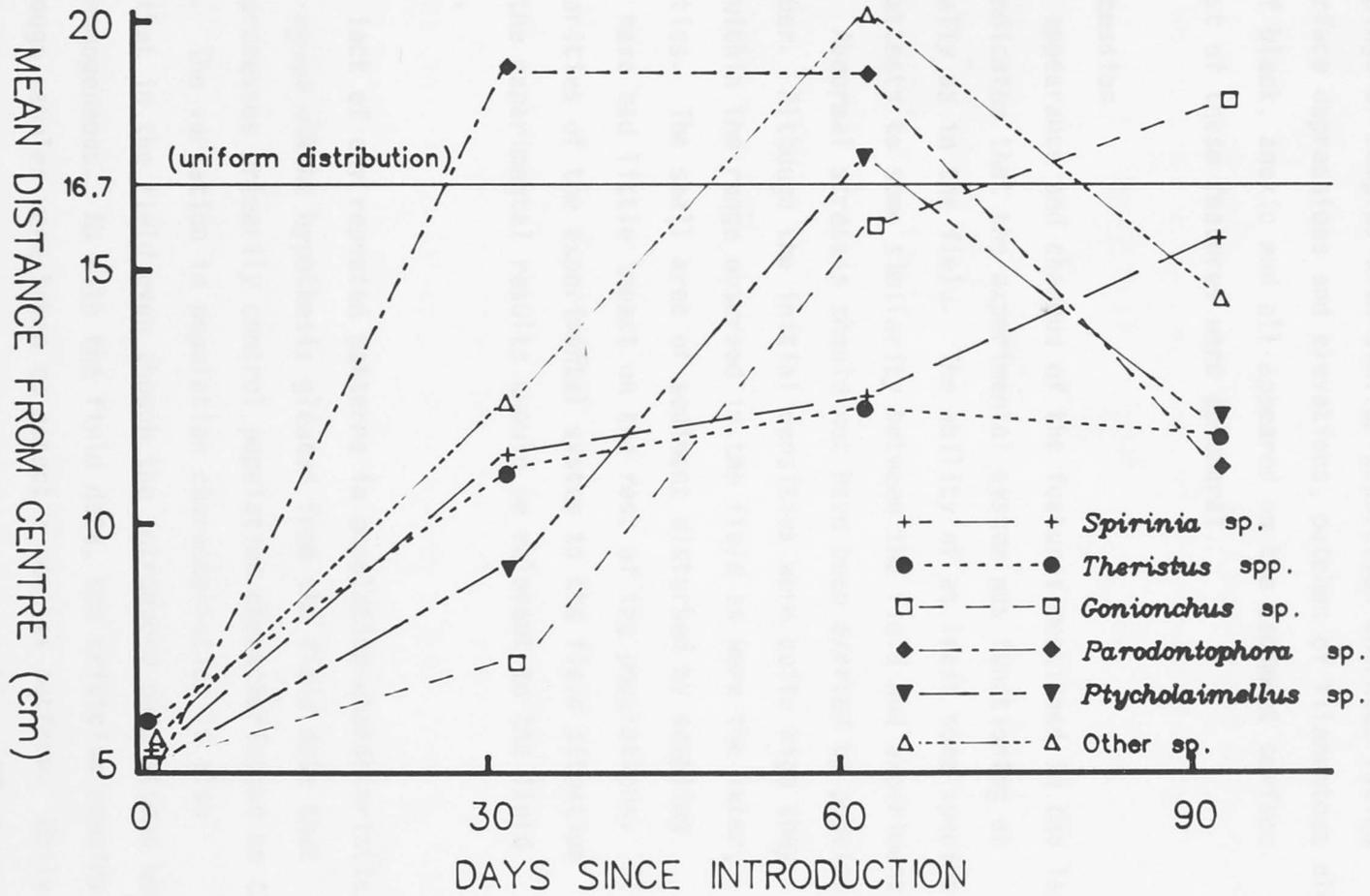


FIGURE 4.5 DISPERSAL OF ABUNDANT SPECIES IN MUD FROM CANDLAGAN CREEK



The variations in abundance of most species were relatively small and most species were present in most samples. There were no obviously strong groupings of samples with similar population characteristics although surface depressions and elevations, patches of filamentous algae and areas of black, anoxic mud all appeared on the sediment surface. However, most of these features were ephemeral.

4.2.4 Discussion

The appearance and changes of the features mentioned in the last paragraph indicates that the experimental system was functioning at least partially as in the field. The ability of at least some species to breed also attests to some similarity between the field and experimental situations. Abnormal stresses should not have been exerted by population density either. Although the initial densities were quite high they were still within the range observed in the field as were the later, lower densities. The small area of sediment disturbed by sampling should also have had little impact on the rest of the populations. All these similarities of the experimental system to the field situation imply that the experimental results should be relevant to the field populations.

The lack of any repeated patterns in population characteristics in any case agrees with the hypothesis gleaned from the field data that stochastic processes primarily control population characteristics on the small scale. The variation in population characteristics is also similar to that in the field even though the introduced populations were originally homogeneous. As with the field data, the criticism remains that not enough samples were taken to detect a complex pattern. While this criticism cannot be answered without enormous sampling effort, any simple pattern should have become evident in the simplified experimental situation and shown up within three months, the sampling interval for the field data. Although there were no simple patterns in population characteristics and probably no complex patterns, the conclusion that

the species occurred in a stochastic manner is not statistically verifiable because no species was sufficiently abundant. Also, the pattern of sampling was not random or replicated sufficiently to allow valid statistical tests.

The apparently random dispersal of the species also supports the conclusion that stochastic processes control population characteristics. Consistent, directed migration was unlikely to be important because no strong aggregations of species, or consistent directional preference in migration were apparent. The species were also not found entirely uniformly, as would occur if there were some form of spacing behaviour or avoidance mechanism. Abnormal stresses were unlikely to be instigating migration for the reasons discussed above. Random movement, however, is very likely to cause slow spread and eventual colonisation of the entire experimental system as was observed.

Two methods of dispersal were probably involved. Some animals were probably transported while suspended in the water column or attached to shifting sediment particles. The few individuals of *Spirina* sp. and *Theristus* sp. and some less common species which were found outside the area of introduction after only 1 hour (time 0, Table 4.3) probably travelled in this way. It is unlikely that they represent contamination of the defaunated sediment: any contamination should have been uniform over all the sediment and no animals were found in the peripheral samples in either tray. Also, the rapidly dispersing species were the same in both experiments - mainly *Spirinia* sp. and the otherwise uncommon *Diplolaimelloides* sp. Exactly the same species escaping is unlikely if the inoculum were escaping from the centre of the tray. However, colonisation of the tray was generally much slower than the high rates suggested by the early observations of these few species, and so it appears that movement in the water column is not the major form of dispersal.

Most species did not colonise the entire tray until day 64, and probably did so mostly by moving through the sediment. The species which dispersed most slowly probably did not disperse by suspension at all. *D. cazca* is a relatively inactive species normally living deep in the mud and *Sabatieria* sp. probably also lives low in the sediment (W.L. Nicholas pers. comm.).

It is widely accepted that nematodes can disperse in both the water column and the sediment (Chandler and Fleeger 1983; Gerlach 1977; Hagerman and Rieger 1981). However, the speed and relative importance of water-borne dispersal seems to depend on how much and how often sediment is suspended and the velocity of local water flows. In North America, defaunated sediment from both littoral and sub-littoral salt-marsh muds were rapidly colonised by suspended nematodes where water flows were considerable (Hagerman and Rieger 1981; Sherman and Coull 1980). However, sub-littoral nematodes from a quiet estuarine salt-marsh were transported poorly in the water column, leaving a 15 x 28 cm area of mud still relatively depopulated compared to surrounding controls even after 29 days for recruitment (Chandler and Fleeger 1983). Conditions of water flow and sediment grain size in my experiment were generally similar to those in the estuary studied by Chandler and Fleeger (1983). Nematode dispersal, by whatever means, was similarly slow. The experimental conditions should also be similar to those in the field. Mangroves typically occur in sheltered estuaries where shallow water, protection from wind and waves and sediment-trapping pneumatophores all limit erosion and redistribution of sediment (Galloway 1982). Both Fullerton Cove and Candlagan Creek are typically quiet. Thus the slow rates of dispersal observed in this experiment, in either type of mud and by whatever means, should at least approximate the field situation. Tidal flows may increase the rate of dispersal or direct migration, however, their effect must remain unknown since the experimental system only very crudely approximated tidal effects.

The rate of dispersal was nevertheless rapid enough to eliminate the possibility of there being patterns on a scale too small to be distinguished. Any patterns on scales much smaller than the sample size would apparently be subject to considerable immigration and probably also emigration. This would seem to preclude any sort of population stability over time and indicate that populations are constantly randomly mixed.

CHAPTER 5

POPULATION PROCESSES ON THE MEDIUM AND LARGE SCALES

5.1 *THE STRENGTH OF DETERMINISTIC PATTERNS*

5.1.1 Introduction

On the medium and large scales of sampling, one or a few key factors seemed to determine most of the population characteristics of the samples at each site; the stochastic variation appeared to occur primarily on the small scale (Chapter 3 and 5). To confirm that little of the stochastic variation occurred on the medium and large scales, the total populations in all the samples at each site were compared. Using the same methods for this analysis as were used for the analysis of the individual samples should also allow the results of the two analyses to be compared. Analysing the total populations at each site should also clarify the patterns in population characteristics among the sites. With most of the population variability due to small scale stochastic processes eliminated by adding the individual samples together, the medium and large scale patterns should be very clear. The patterns should also account for most of the variance if the deterministic patterns are indeed predominant on the medium and large scales and little stochastic variation occurs.

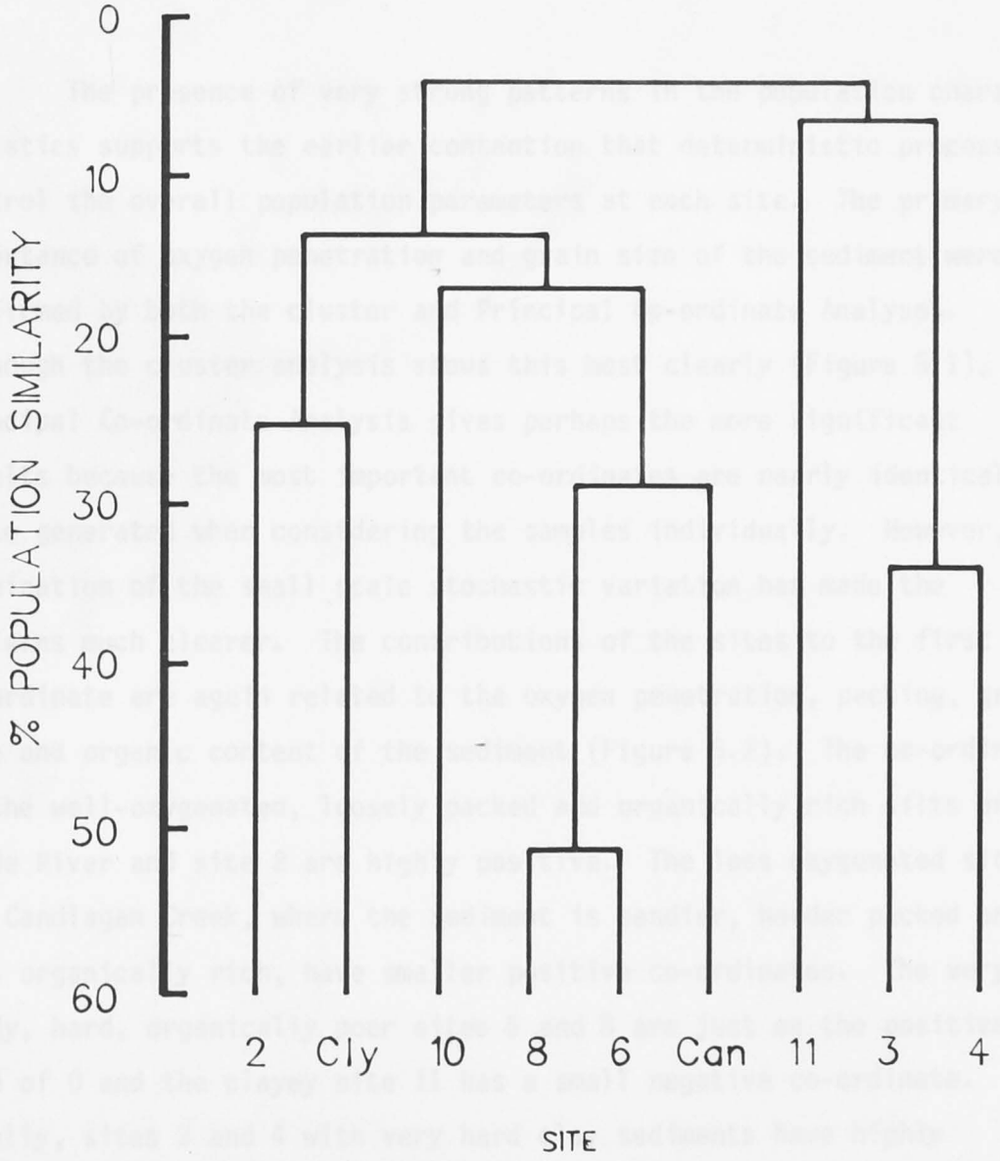
5.1.2 Method

Using the total density of each species at each of the nine sites, cluster and Principal Co-ordinate Analyses were carried out as in Chapter 3.

5.1.3 Results

The dendrogram produced by cluster analysis (Figure 5.1) clearly indicates the strong relationship of population characteristics at each site to the grain size and oxygen penetration characteristics of the sediment - the same factors which were identified earlier. The principal

FIGURE 5.1 RELATIONSHIPS AMONG THE TOTAL POPULATIONS AT EACH SITE: CLUSTER ANALYSIS



co-ordinates were also very similar to the most important co-ordinates in the analysis of the individual samples (Table 5.1; Figures 5.2 - 5.5). The first three co-ordinates accounted for more than 50% of the total variance.

The presence of very strong patterns in the population characteristics supports the earlier contention that deterministic processes control the overall population parameters at each site. The primary importance of oxygen penetration and grain size of the sediment were confirmed by both the cluster and Principal Co-ordinate Analyses. Although the cluster analysis shows this most clearly (Figure 5.1), the Principal Co-ordinate Analysis gives perhaps the more significant results because the most important co-ordinates are nearly identical to those generated when considering the samples individually. However, the elimination of the small scale stochastic variation has made the patterns much clearer. The contributions of the sites to the first co-ordinate are again related to the oxygen penetration, packing, grain size and organic content of the sediment (Figure 5.2). The co-ordinates of the well-oxygenated, loosely packed and organically rich silts of the Clyde River and site 2 are highly positive. The less oxygenated site 10 and Candlagan Creek, where the sediment is sandier, harder packed and less organically rich, have smaller positive co-ordinates. The very sandy, hard, organically poor sites 6 and 8 are just on the positive side of 0 and the clayey site 11 has a small negative co-ordinate. Finally, sites 3 and 4 with very hard clay sediments have highly negative co-ordinates.

The second principal co-ordinates has a similar trend except that the organically poor sites (6, 8 and Candlagan Creek) have highly negative co-ordinates and the most organically rich sites (the Clyde River and sites 2 and 4) have highly positive co-ordinates (Figure 5.3). The third co-ordinate seems to relate to surface water as well as the grain size characteristics of the sediment (Figure 5.4). Site 11 has a

TABLE 5.1 Proportion of Variance of Principal Co-ordinates - Total Site Populations

	Principal Co-ordinate							
	1	2	3	4	5	6	7	8
% Variance	18.7	17.5	14.0	13.1	10.7	10.0	9.1	6.8

FIGURE 5.2 VALUES OF SITES ON FIRST PRINCIPAL CO-ORDINATE

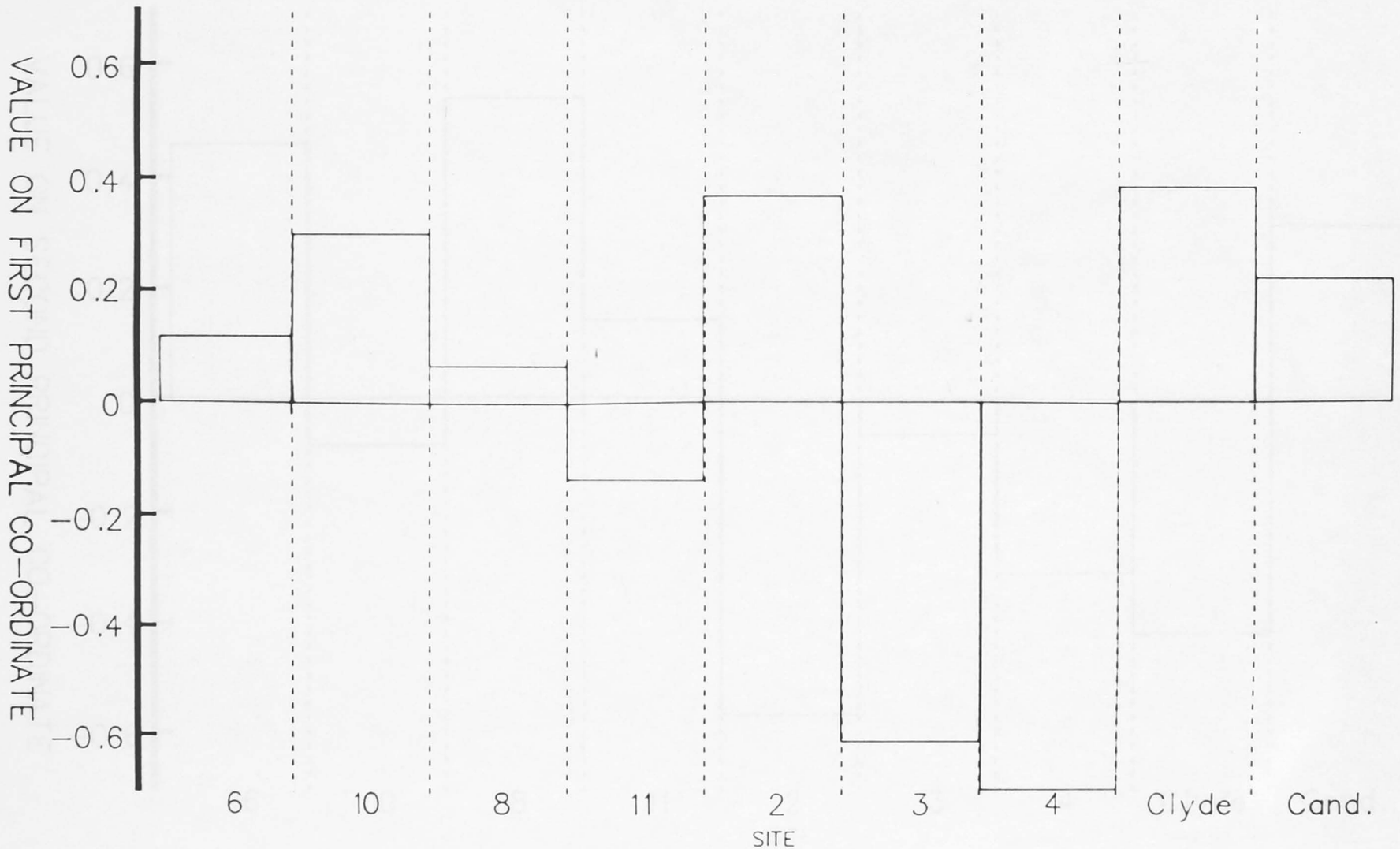


FIGURE 5.3 VALUES OF SITES ON SECOND PRINCIPAL CO-ORDINATE

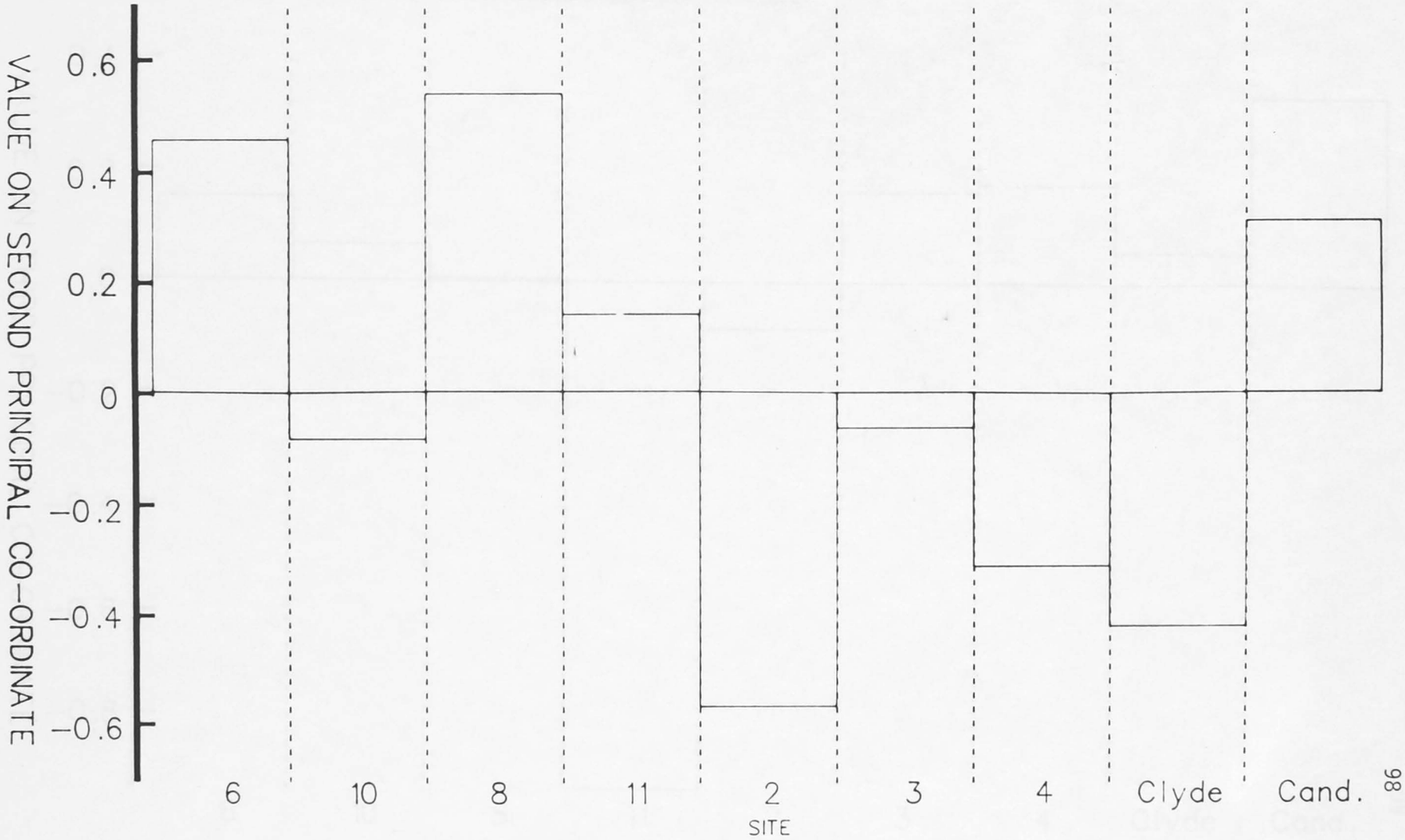


FIGURE 5.4 VALUES OF SITES ON THIRD PRINCIPAL CO-ORDINATE

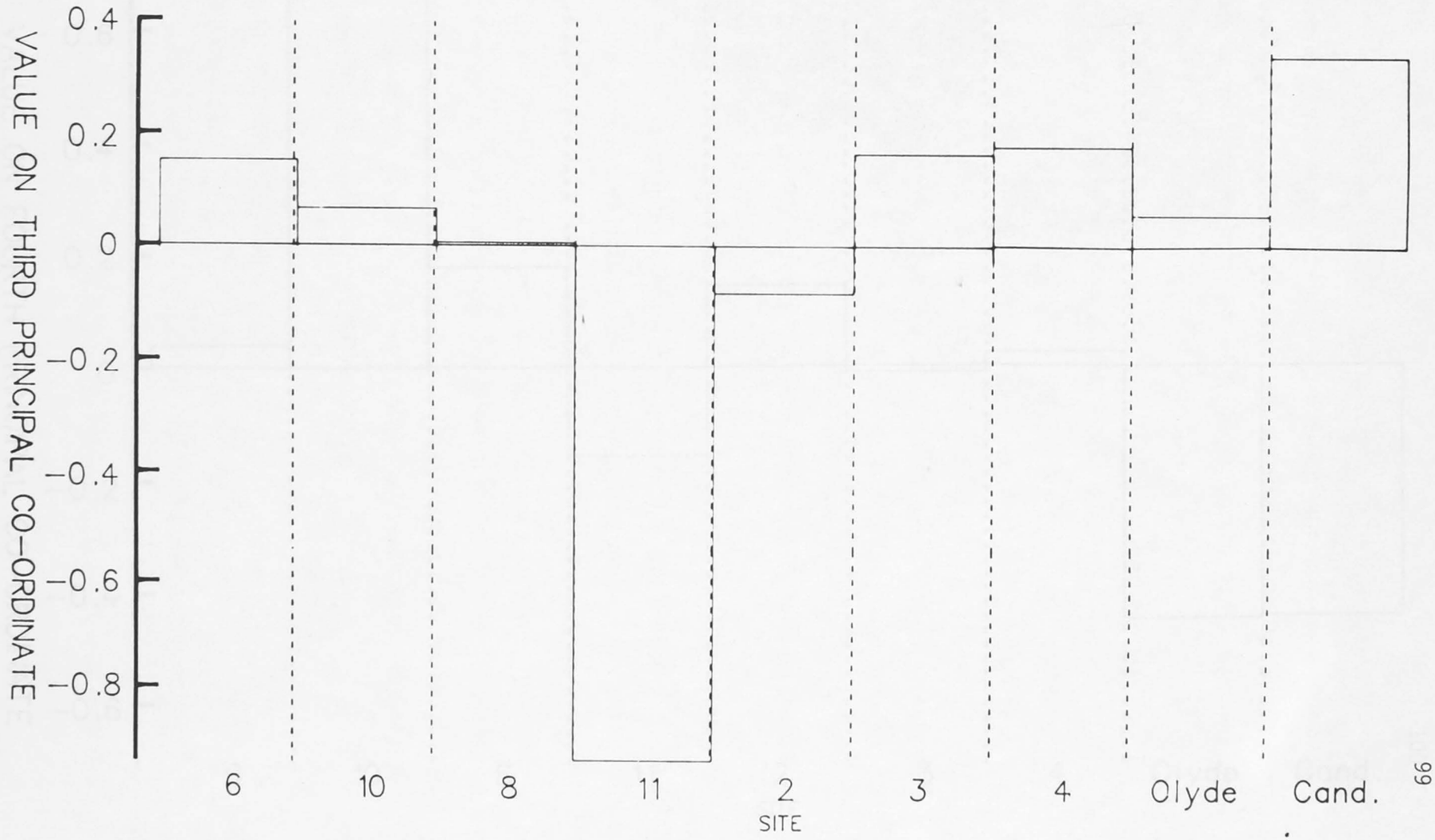
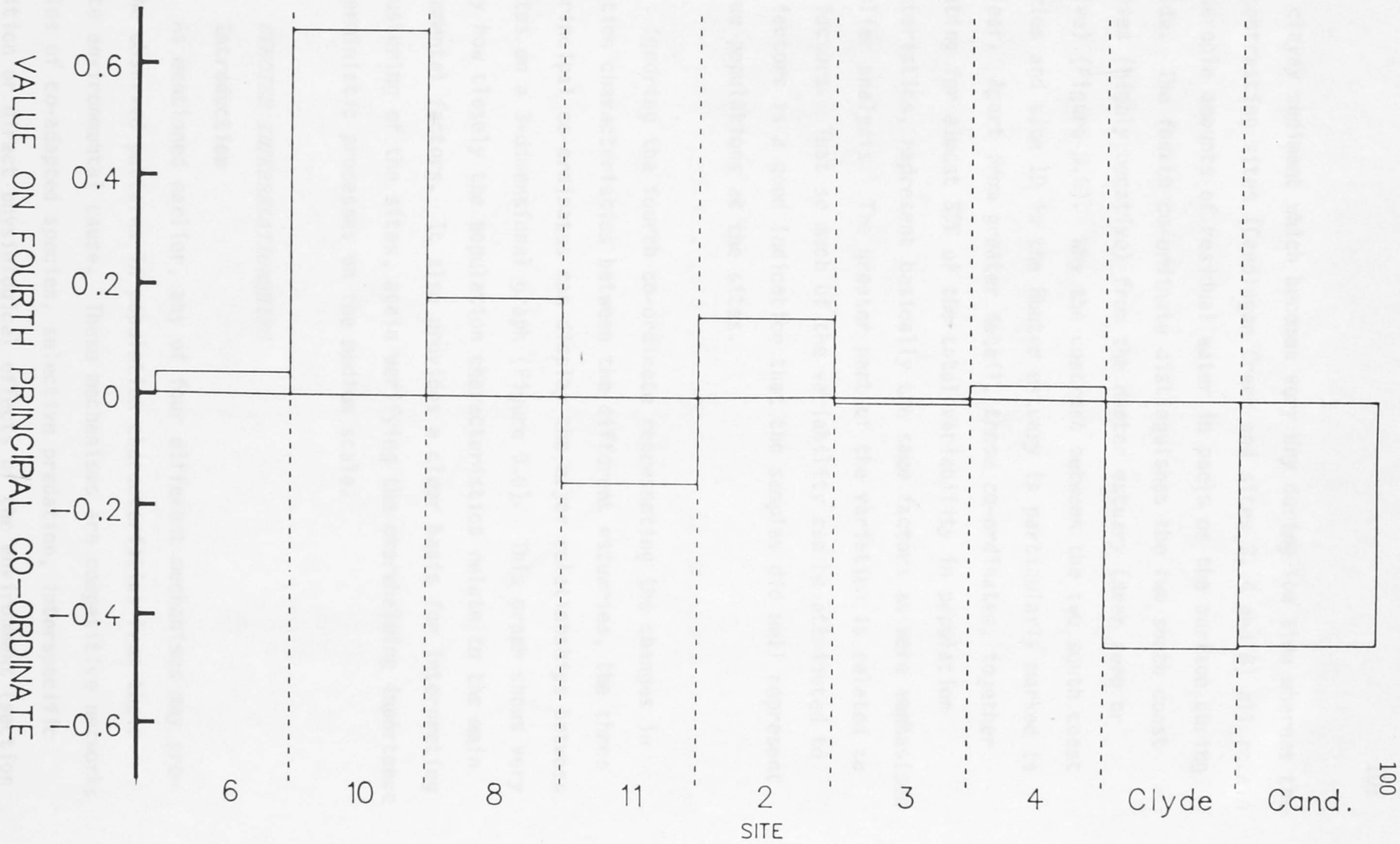


FIGURE 5.5 VALUES OF SITES ON FOURTH PRINCIPAL CO-ORDINATE



hard, clayey sediment which becomes very dry during low tide whereas the most contrasting sites (Candlagan Creek and sites 3, 4 and 6) all retain considerable amounts of residual water in pools on the surface during low tide. The fourth co-ordinate distinguishes the two south coast estuaries (highly negative) from the Hunter estuary (near zero or positive) (Figure 5.5). Why the contrast between the two south coast estuaries and site 10 in the Hunter estuary is particularly marked is not clear. Apart from greater detail, these co-ordinates, together accounting for almost 65% of the total variability in population characteristics, represent basically the same factors as were emphasised by earlier analysis. The greater part of the variation is related to these factors. That so much of the variability can be attributed to these factors is a good indication that the samples did well represent the true populations at the sites.

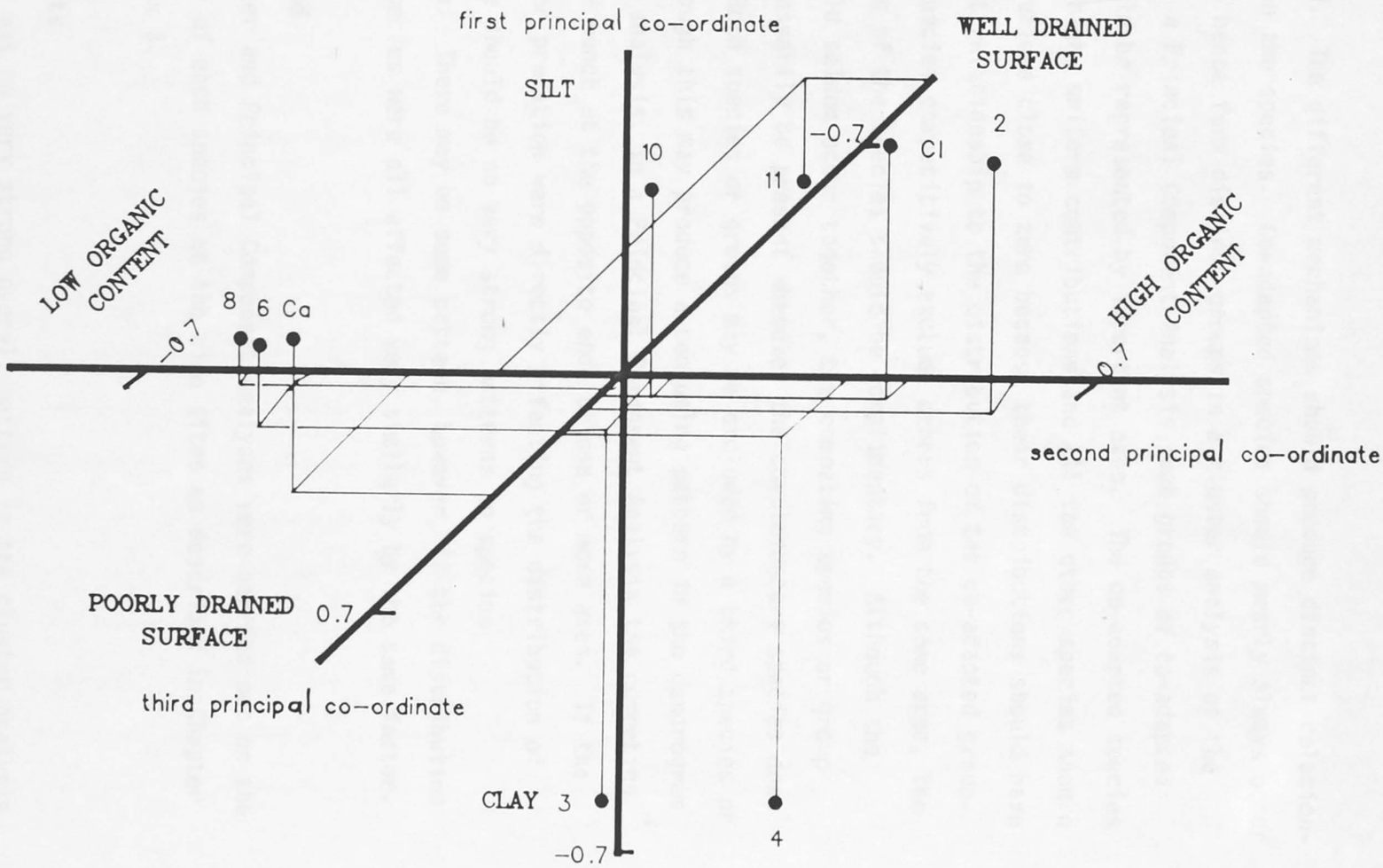
Ignoring the fourth co-ordinate representing the changes in population characteristics between the different estuaries, the three main principal co-ordinates can display the major relationships between the sites on a 3-dimensional graph (Figure 5.6). This graph shows very clearly how closely the population characteristics relate to the main environmental factors. It also provides a clear basis for interpreting the clustering of the sites, again verifying the overwhelming importance of deterministic processes on the medium scale.

5.2 *SPECIES INTERRELATIONSHIPS*

5.2.1 **Introduction**

As mentioned earlier, any of four different mechanisms may produce the observed patterns in population characteristics from their ultimate environmental cause. These mechanisms are competitive networks or guilds of co-adapted species, selective predation, interspecific competition or direct physiological effects of the environment (section 1.3). A way to distinguish which mechanism is likely to be operating in the field is by examining how the distributions of the different species

FIGURE 5.6 POSITION OF SITES IN THE SPACE OF THE FIRST THREE PRINCIPLE CO-ORDINATES



were related. The different mechanisms should produce distinct relationships between the species. Co-adapted species should nearly always occur together and hence form distinct groups in a cluster analysis of the species. In a Principal Component Analysis such groups of co-adapted species should be represented by important axes. The co-adapted species should have high, uniform contributions and all the other species should have contributions close to zero because their distributions should have no consistent relationship to the distribution of the co-adapted group. If certain species competitively exclude others from the same area, the distributions of the species should be complimentary. Although the species should seldom occur together, the competing species or group need not necessarily be present whenever the complementary species does not occur. Both species or groups may be excluded by a third species or group. Although this may produce a confusing pattern in the dendrogram of a cluster analysis, in a Principal Component Analysis the competing groups should bunch at the opposite ends of one or more axes. If the environment or predation were directly affecting the distribution of species there should be no very strong patterns in species distributions. There may be some pattern, however, if the distribution of several species were all affected very similarly by the same factor.

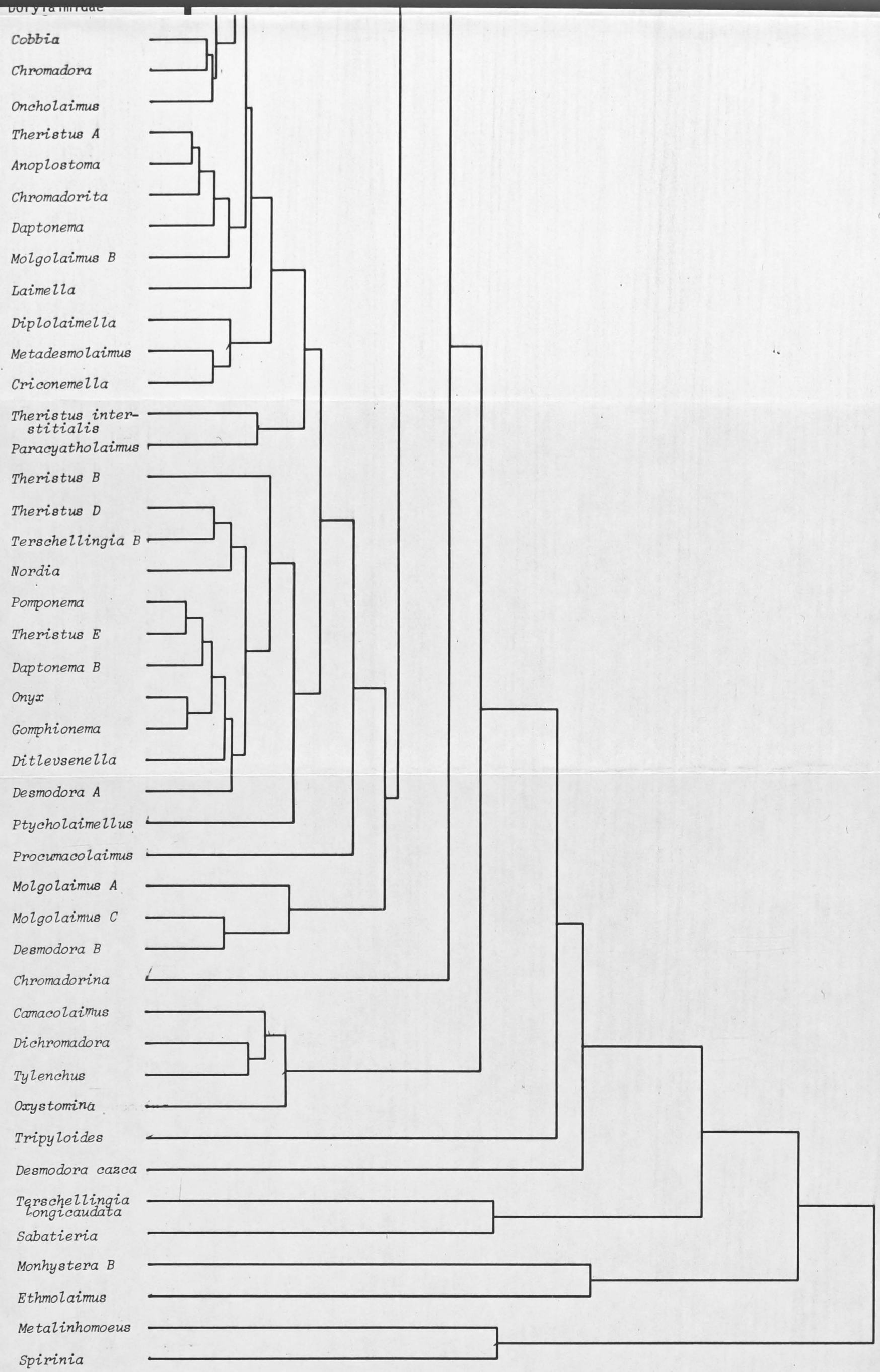
5.2.2 **Method**

Cluster and Principal Component analyses were carried out on the total density of each species at the nine sites as described in Chapter 2 and Appendix 3.

5.2.3 **Results**

There was no very strong overall pattern in the cluster analysis (Figure 5.7). However, many species had very similar distributions and so grouped very tightly on the dendrogram. These tightly grouped species (eg. *Antomicron* sp. and *Diplopeltis* sp.) were generally very rare species which happened to occur at very low densities at the same site(s). Species occurring at slightly higher densities and more sites gradually

FIGURE 5.7 DENDROGRAM SHOWING CLUSTERING OF ALL SPECIES


Cobbia
Chromadora
Oncholaimus
Theristus A
Anoplostoma
Chromadorita
Daptonema
Molgolaimus B
Laimella
Diplolaimella
Metadesmolaimus
Criconemella
Theristus interstitialis
Paracyatholaimus
Theristus B
Theristus D
Terschellingia B
Nordia
Pomponema
Theristus E
Daptonema B
Onyx
Gomphionema
Ditlevsenella
Desmodora A
Ptycholaimellus
Procumacolaimus
Molgolaimus A
Molgolaimus C
Desmodora B
Chromadorina
Camacolaimus
Dichromadora
Tylenchus
Oxystomina
Tripyloides
Desmodora cazca
Terschellingia longicaudata
Sabatieria
Monhystera B
Ethmolaimus
Metalinhomoeus
Spirinia

joined these rare species. Most species were grouped in this way. However, several groups of species with distinctive distributions were identified (Figure 5.8). Even these most distinct species groups had distributions more than 60% similar.

Three principal component axes accounted for almost 95% of the total variance in species distributions (Table 5.2). Only six species (of the 89) made important contributions to these axes. *Tripyloides* sp. and *Desmodora cazca* made a positive contribution to the first axis, *Monhystera* sp. and *Diplolaimelloides* sp. a negative contribution (Figure 5.9). *Monhystera* sp. and *Diplolaimelloides* also made important contributions to the second axis, however no other species were involved. *Terschellingia longicaudata* and *Sabatieria* sp. were the only species to make important contributions to the third axis.

5.2.4 Discussion

The lack of any pattern in the distributions of most species in the cluster analysis, plus the contribution of only a few species to the important principal component axes, indicates that groups of co-adapted species are not important in determining population characteristics. Competition was also unlikely to be important. Apart from the first axis, only two species made major contributions to each axis and these contributions were similar, not opposite in sign. The rest of the species made almost no contribution. Even though *Monhystera* sp. and *Diplolaimelloides* sp. made opposite contributions to the other species on the first axis, their contributions to the second axis were much greater, indicating that much of their distribution is independent of the distribution of *Tripyloides* sp. and *Desmodora cazca*. The independent nature of the distributions of these two species pairs is emphasised on the 3-dimensional plot (Figure 5.9).

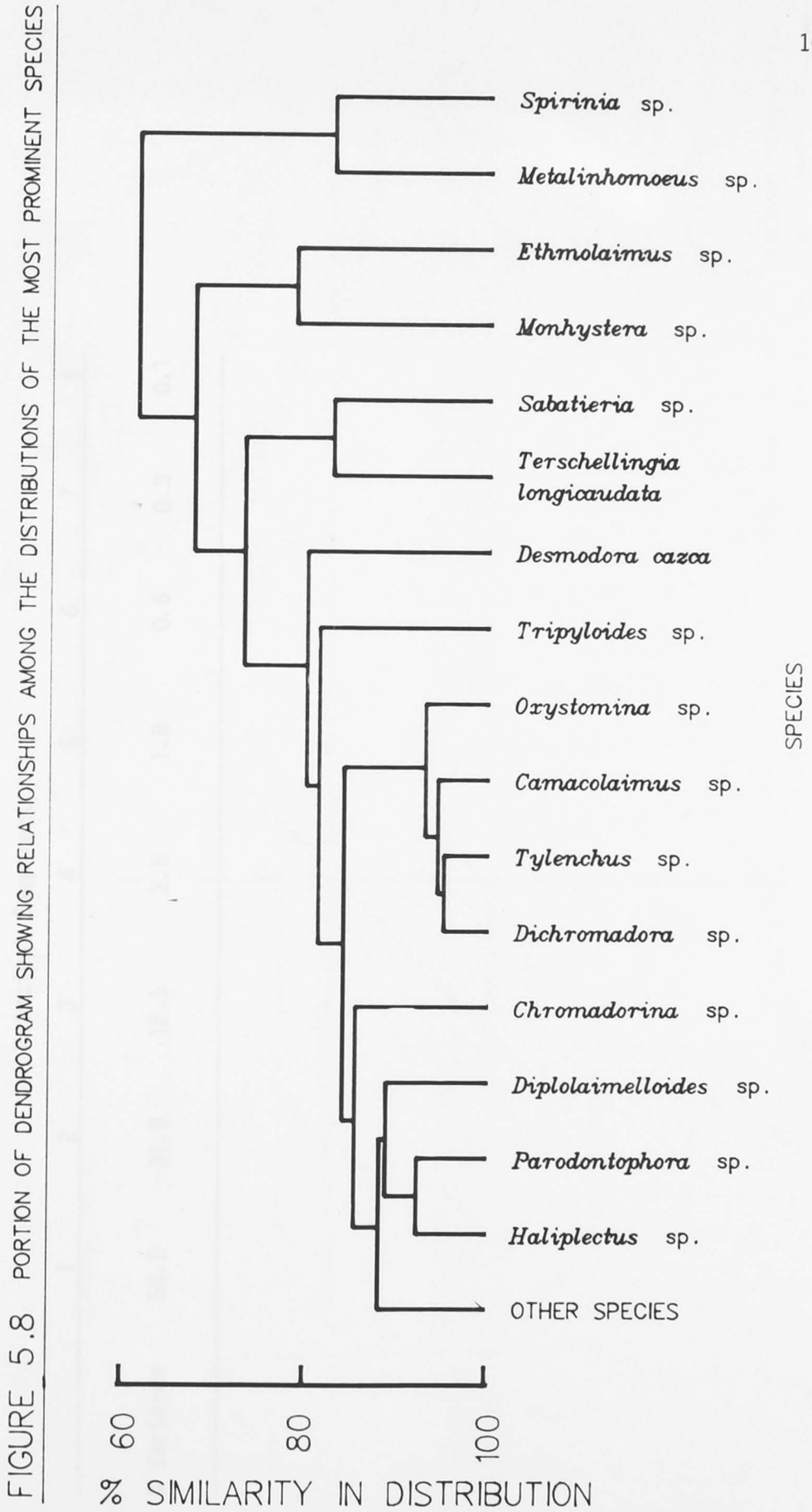
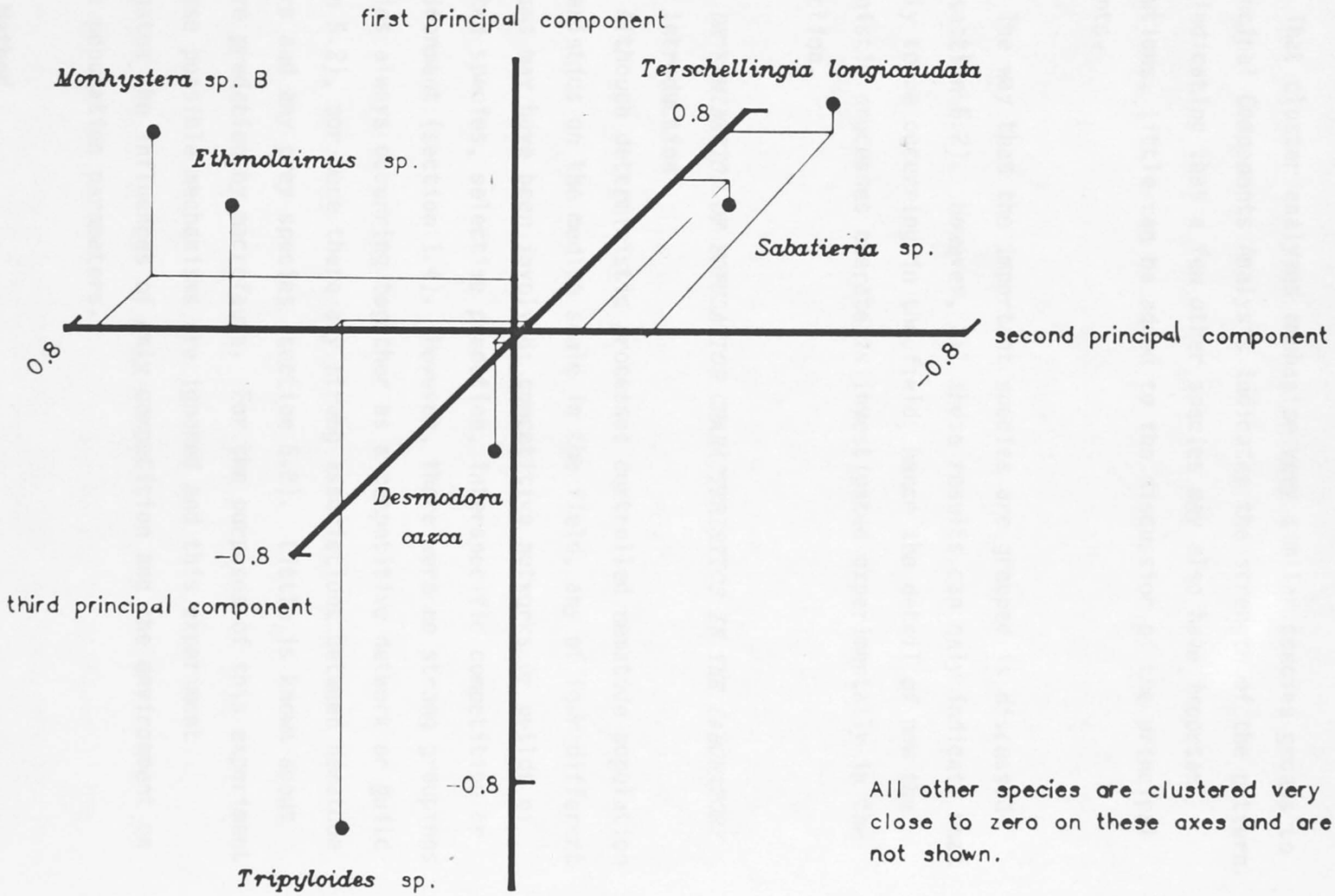


FIGURE 5.8 PORTION OF DENDROGRAM SHOWING RELATIONSHIPS AMONG THE DISTRIBUTIONS OF THE MOST PROMINENT SPECIES

TABLE 5.2 Proportion of Variance of Principal Components - Total Site Populations

	Principal Component							
	1	2	3	4	5	6	7	8
% Variance	50.5	31.8	12.5	2.5	1.8	0.6	0.3	0.1

FIGURE 5.9 POSITION OF MOST PROMINENT SPECIES IN THE SPACE OF THE FIRST THREE PRINCIPAL COMPONENTS



All other species are clustered very close to zero on these axes and are not shown.

That cluster analyses emphasise very similar species groups to the Principal Components Analysis indicates the strength of the pattern. Beyond indicating that a few other species may also have important distributions, little can be added to the discussion of the principal components.

The way that the important species are grouped is discussed later (section 6.2). However, all these results can only indicate what is likely to be occurring in the field, hence the detail of how the deterministic processes operate is investigated experimentally in the next section.

5.3 *DETERMINATION OF POPULATION CHARACTERISTICS IN THE LABORATORY*

5.3.1 Introduction

Although deterministic processes controlled nematode population characteristics on the medium scale in the field, any of four different mechanisms may have been involved; competitive networks or guilds of co-adapted species, selective predation, interspecific competition or the environment (section 1.4). However, there were no strong groupings of species always occurring together as a competitive network or guild (section 5.2), nor were there any strong associations between nematode predators and any prey species (section 5.2). Little is known about selective predation by macrofauna. For the purposes of this experiment both these possible mechanisms are ignored and this experiment investigates the influences of only competition and the environment on nematode population paramaters.

5.2.2 Method

Two identical experimental trays were used, each containing a 2 square by 3 square chequerboard pattern of defaunated muds from sites 2 and 8. In one tray the nematodes extracted from both muds were reintroduced into the two squares of mud at one end of the tray. However, the nematodes from site 2 only were reintroduced into the

equivalent squares of the other tray. Three months later two random samples were taken from each square of mud. Three months should be ample time for the animals to disperse (section 4.2). Random co-ordinates were chosen from a table of random numbers (Fisher and Yates 1957) and located using a wire mesh overlaying the tray which divided each square into a 10 x 10 unit grid. The distribution of the frequently occurring species in the trays was compared by an Analysis of Variance after transforming the densities of each species in each sample by taking the square root. The rationale of this procedure to make the data approximate a normal distribution is discussed later. A similar experiment was run concurrently using muds from the Clyde River and Candlagan Creek sites. The Candlagan Creek nematodes were used alone. These two combinations of sites were chosen because the members of each pair were quite faunistically distinct so the effect of whatever is causing the differences in population characteristics is likely to be strong. Relatively few species were shared within the pairs of sites and most of the species in common normally occurred at very disparate densities.

5.3.3 **Rationale of Method**

If the sedimentary environment affects the nematode populations directly, there should be no difference in the distribution of nematodes in the trays of each pair because the mud environments of each were, as far as possible, identical. However, if competition controls the distribution and abundance of the frequently occurring nematode species, the distribution of nematodes in the two trays should be different: the indigenous species should competitively dominate the immigrant species when both are present, but when the nematodes from only one site are present, these species should colonise both types of mud without competitive impediments.

5.3.4 Results

Most species occurred very sporadically. However, a few species occurred frequently enough in both trays of each pair to compare densities. The densities of these species varied considerably among samples (Table 5.3). However, which other species were present did not affect the distribution of any frequently occurring species in the trays of either pair (Table 5.4). The species present also had no significantly different effect on any species density in the different mud types in either experiment (there was no interactive effect of mud type and the origin(s) of the nematodes present). However, in the experiments on sites 2 and 8, both *D. cazca* and *Sabatieria* sp. were significantly more numerous in their local sediment, although not entirely restricted to it. A similar trend was apparent in *Spirinia* sp., *Theristus* spp. and *Gomphionema* sp. in the Candlagan Creek/ Clyde River experiment (Table 5.4), but the differences in density between the two sediments were never statistically significant (Table 5.4). The density of *Molgolaimus* sp. did not differ consistently between the two sediments. There were no consistent differences in the density of any frequently occurring species between the squares into which nematodes were introduced and those they were not, although this could not be tested statistically. The density of the abundant species was never significantly correlated between the two replicate samples within each square. Occasional individuals of species from the sites whose fauna were not introduced alone were found in both sediments of each tray.

5.3.5 Discussion

The nature of the mud environment rather than interspecific competition limited the distribution of both *D. cazca* and *Sabatieria* sp. in the site 2/8 experiment. Competition was also unimportant in determining the distribution of the Candlagan Creek nematodes *Sprinia* sp., *Theristus* spp., *Gomphionema* sp. and *Molgolaimus* sp. However, the mud environment had no statistically significant effect on any of these

TABLE 5.3 Densities of abundant species in competition experiments

Species	Feeding Category	Nematodes Present	Mud Type	Number of Animals per Sample — Square Number (replicate number) 1(1)	(2)	2(1)	(2)	3(1)	(2)	Mean Density
Desmodora cazca	2a	2	2	18	18	14	21	20	14	17.5
			8	7	6	1	5	5	2	4.3
		2 and 8	2	19	14	6	16	8	19	13.7
			8	2	3	2	5	0	6	3.0
Sabatieria sp.	1b	2	2	11	10	4	8	9	14	9.3
			8	0	1	2	3	5	0	3.3
		2 and 8	2	6	21	19	12	7	13	13.0
			8	4	2	0	1	0	1	2.7
Spirinia sp.	2a	Candlagan Ck	Cand.	0	10	8	3	9	6	6.0
			Clyde	2	4	0	0	5	3	2.3
		Cand. & Clyde	Cand.	3	8	0	2	7	9	4.8
			Clyde	2	4	0	0	1	4	2.3
Theristus spp.	1b	Candlagan Ck	Cand.	9	9	6	1	4	11	6.7
			Clyde	0	2	1	7	4	2	2.7
		Cand. & Clyde	Cand.	0	4	6	10	2	6	4.7
			Clyde	3	2	4	4	3	0	2.7
Gomphionema sp.	2a	Candlagan Ck.	Cand.	6	5	0	9	5	0	4.2
			Clyde	0	0	3	1	1	1	1.2
		Cand. & Clyde	Cand.	9	0	2	4	6	7	4.7
			Clyde	0	0	0	4	4	6	2.3
Molgolaimus sp.	2a	Candlagan Ck.	Cand.	2	0	5	0	2	0	1.5
			Clyde	2	2	5	0	2	0	3.0
		Cand. & Clyde	Cand.	5	0	4	8	0	3	3.3
			Clyde	1	0	1	3	0	6	1.8

TABLE 5.4 Statistical Effects of Factors in Competition Experiments

Source of Variation	F-Ratio		
	Species Present	Mud Type	Species Present & Mud Types
Species			
Desmodora cazca	3.1	56.2 *	0.0
Sabatieria sp.	0.3	48.7 *	1.0
Spirinia sp.	0.0	3.4	0.2
Theristus spp.	0.4	4.0	0.7
Gomphionema sp.	0.3	3.3	0.7
Molgolaimus sp.	0.0	0.1	2.0

* - indicates statistical significance, $P < 0.05$ (df=1, 20)

species despite a trend toward higher densities of the first three species in their local mud. It is possible that this trend occurred purely by chance, but it is unlikely that three species should be similarly affected. Any effect of the mud environment may have been obscured by the variation in the densities of all four abundant species, even between samples from the same square. Such variation, also observed in the dispersal experiment (section 4.2) and in the field (section 3.1), was probably an indication of the stochastic processes which randomly mix species on a small scale.

The lesser effect of the environment in the Candlagan Creek/Clyde River experiment seems most likely to reflect less ecological and faunal distinctness between the sites. The Candlagan Creek and Clyde River estuaries shared more species in common than sites 2 and 8. Although much more abundant at Candlagan Creek, some *Spirinia* sp., *Theristus* spp. and *Gomphionema* sp. were also found in the samples from the Clyde. Notably, *Molgolaimus* sp., which showed no consistent differences in density between the Candlagan Creek and Clyde River muds in the experiment, was similarly abundant at both field sites. However, *D. cazca*, which occurred at very disparate densities in the experiment, was abundant at site 2 but totally absent from site 8. *Sabatieria* sp., which also differed greatly in density between the experimental muds, was abundant at site 2 but very rare at site 8.

There are many alternative and perhaps additional explanations for the lack of any significant effect of the environment in the Candlagan Creek/Clyde River experiment. The sedimentary environment(s) in the experiment may have been changed by the defaunation process. Although such changes cannot be entirely ruled out, it seemed unlikely that they were of much importance since all the species used for comparisons were abundant and seemed to survive and disperse quite well during this experiment, as they did in the other laboratory experiment (section 4.2). The absence of macrofauna could be more important at

Candlagan Creek and the Clyde River. However, there seems no obvious reason why this should be so. It is also possible that some environmental factor which is not associated with the sediment may be the primary cause of distributional patterns of the species from the Candlagan and Clyde estuaries and that the sedimentary environment is only a secondary, weak influence. However, it seems unlikely given the strong parallels between the patterns in the field populations and the sediment characteristics.

The probable feeding habits of the species in this experiment may be of importance. Alongi and Tietjen (1980) observed competition between two nematode species classified as selective deposit feeders by Wieser (1953) and Boucher (1973). However, all of the abundant species in my experiment were in other feeding categories (Table 5.3), and were generally representative of the species which were abundant in the field. Alongi and Tietjen found that an epistrate feeder, similar to several species in my experiment, did not compete with selective deposit feeders, and some consider that competition is important only between selective deposit feeders (Tietjen 1977; Tietjen and Lee 1977). As selective deposit feeders were not overwhelmingly abundant at any of the sites, it seems that if selective deposit feeders do compete, this is unlikely to be very important in determining the characteristics of the entire population.

Although the conditions of Alongi and Tietjen's (1980) experiment were more rigorous than the present experiment, it is not clear how similar their conditions were to the field. One species of chlorophyte alga and two species of bacteria were used in a closed, confined environment with only three species of nematodes present. The conditions in my experiment should be more comparable to the field. However, they were not totally similar to field conditions: the normal tidal cycle and macrofauna were absent, and the densities of animals were a little lower than normal for the field. Time and equipment limitations

and the inefficiency of extraction procedures prevented a closer approach to reality in these aspects. However, the densities of *D. cazca* and *Sabatieria* sp. overlapped somewhat between the field and experimental samples from their local muds. Although the other species were always less dense in the experiment than in the field, their densities all came within about two individuals per cm^2 of the field samples. The absence of macrofauna and tides may limit the generality of the present results, however, the major result that sediment affects distribution remains. Macrofaunal and tidal influences may have made the species distributions closer to those in the field, but the experimental distributions in this experiment were still qualitatively the same.

The species may compete at higher densities, but, there is no evidence that the species are competing at the present densities. If competition does occur, it would be unlikely to be effective until much higher densities were attained, unless there is some sort of threshhold effect at which competition suddenly becomes intense. This seems unlikely.

Which component of the environment caused the differences in density of *D. cazca* and *Sabatieria* sp. is not certain. Although the sediment grain size is the most obvious difference between the sediments in each tray pair, many other ecological factors are associated with grain size (section 1.4). However, whichever environmental factor caused the differences in density, it is important that its effects did not absolutely preclude any of the abundant species from the foreign mud type, at least over the range of mud conditions in this experiment. This, and the lack of any effect by the sedimentary environment on the distribution of *Molgolaimus* sp. are discussed in Chapter 6.

CHAPTER 6

GENERAL DISCUSSION

6.1 *A SYNTHESIS OF RESULTS*

6.1.1 Introduction

All the results of this project combine to give a general picture of the population processes affecting estuarine littoral nematodes. Both deterministic and stochastic processes are important, however they act mainly on different spatial scales. The population changes over certain of these scales are more important than others.

6.1.2 The Large Scale

Changes in population characteristics between estuaries in different regions of the NSW coast are relatively unimportant. On this, the largest scale investigated, there are at least some major changes in populations which can be represented by a single important principal co-ordinate. However, the changes represent only about 5% of the total variability in population characteristics. This percentage may have been increased by sampling more estuaries with greater distances between them, but even this is unlikely to greatly enhance the importance of population changes on this scale. Only 12 species, mostly rare, were limited to the Clyde River and Candlagan Creek estuaries whereas many species occurred at quite similar densities at environmentally similar sites in both the central and south coast estuaries. This suggests that the variation in population characteristics among different sites within a single estuary is much more important than changes due solely to factors associated with the location of the estuary, such as water temperature.

Which ecological process(es) were operating on this scale cannot be resolved because only two regions were sampled and so little variation was observed between the different estuaries.

6.1.3 The Medium Scale

The changes in population characteristics between different sites are very important, accounting for about 50% of the total variability. Deterministic processes are most important on this, the medium scale.

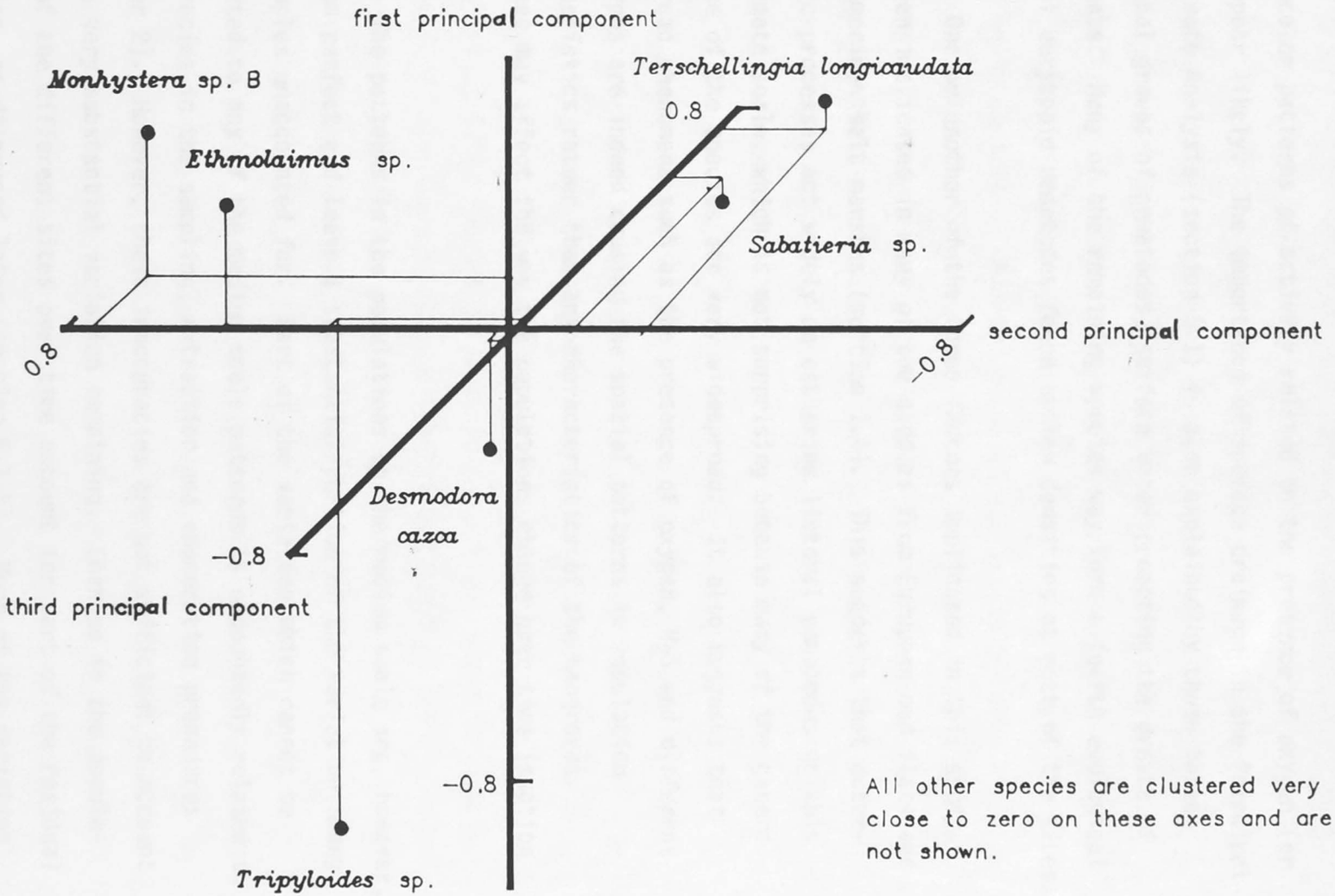
The pattern of dispersal proposed here is consistent with the action of deterministic processes, being slow enough for even quite subtle patterns to develop without constant intermixture with populations from surrounding areas. The factors implicated in causing the deterministic patterns, mainly associated with the sediment grain size, do not appear to change rapidly enough for this slow dispersal to be any problem to the animals in locating suitable habitat. Indeed, that dispersal of nematodes suspended in the water column is probably necessary for extensive dispersal also makes stochastic processes unlikely on this scale. The nematodes deposited from suspension at any site are likely to be controlled by the same hydrodynamic forces which control the grain size of the sediment, unless of course the nematodes here have much greater control over water-borne dispersal than has been previously observed elsewhere.

The importance of physical characteristics of the sediment is not surprising. The redox potential, organic content and grain size distribution of the sediment are strongly associated in the field and probably in turn affect the distribution of potential foods as well. The ranges of these factors can also be very wide, even within a single estuary. In the Hunter estuary, the depth at which the redox potential of the sediment drops below $^{-}300$ mV varies from only a few millimetres to over 10 cm. This means that the 6 cm deep samples may have been almost all poorly oxygenated or almost all well oxygenated. The organic content of the sediment varied from a few percent to over 10 per cent, with even larger relative changes if the distribution of carbon is considered. The median grain size of the sediment varied by almost two orders of magnitude.

Of the three related environmental factors related to the changes in population characteristics, only two appear to have any direct effect on the nematodes. The grain size of the sediment seems unlikely to have any major direct effect on the populations. At least in the experiment on competition (section 5.2), physical restrictions on movement seemed unlikely since the species moved into two sediments of vastly different grain size. Behavioural movement may have occurred in the experiment, but seems unlikely in the field because the gradients in grain size are much less steep and the distances to be moved very much greater than in the experiment. In the field, the movement and deposition of nematodes of different sizes and densities may have been controlled by the same hydrological forces governing grain size. However, this is unlikely in *Desmodora cazca* and *Sabatieria* sp. which were strongly affected by the sediment under experimental conditions where dispersal in suspension was unlikely.

Oxygen availability and food are much more likely to affect population characteristics, however, their effects are complex, and are reflected in the distributions of the most variable species. The six species which make major contributions to the first three principal components (repeated here as Figure 6.1) form distinct ecological groups based on food requirements and oxygen availability. *Monhystera* sp. and *Ethmolaimus* sp. form one group and are both associated with surface algae (W.L. Nicholas, pers. comm.). *Sabatieria* sp. and *Terschellingia longicaudata* are thought to live deeper in the mud, from preliminary stratified sampling (Hodda & Nicholas, unpublished data). The third group, *Desmodora cazca* and *Tripyloides* sp., probably represent aerobic sediment dwellers since they are found at highest densities in well oxygenated sediments (site 12 and the Clyde River). However, food may also be involved since these sites also had high proportions of fine particulate carbon which is probably related to certain food types. Just how oxygen availability or hydrogen sulphide concentration affect these species warrants future investigation, although physiological

FIGURE 6.1 POSITION OF MOST PROMINENT SPECIES IN THE SPACE OF THE FIRST THREE PRINCIPAL COMPONENTS



All other species are clustered very close to zero on these axes and are not shown.

tolerance or patterns of activity related to the presence of oxygen (or H_2S) appear likely. The importance of surface drainage in the Principal Co-ordinate Analysis (section 5.1) is also explained by these three ecological groups of nematodes, surface water promoting the growth of algal mats. Many of the remaining species may form a fourth ecological group of eurytopic nematodes found at low densities at most of the sites.

One or another of the three factors implicated in this study have been implicated in many of the studies from European mud flats and North American salt marshes (section 1.4). This suggests that deterministic processes act widely on estuarine littoral nematodes on this approximate scale, which is not surprising because many of the genera and some of the species are very widespread. It also suggests that widespread phenomena such as the presence of oxygen, H_2S and different food types are indeed causing the spatial patterns in population characteristics rather than any characteristics of the mangroves. Mangroves may affect the way the populations change over time (section 6.1.5)

The patterns in the populations on the medium scale are, however, far from perfect and leave a substantial portion of the variation among the samples unaccounted for. Part of the variation which cannot be attributed to any of the medium scale patterns is undoubtedly related to inaccuracies in the sampling, extraction and enumeration procedures (Chapter 2). However, these inaccuracies are not sufficient to account for the very substantial variation remaining. Changes in the populations of the different sites over time account for part of the residual variation, as discussed later (section 6.1.5). Much of the variation not attributable to medium (or large) scale patterns is, however, due to population processes acting at smaller scales within the medium scale pattern.

6.1.4 The Small Scale

About 35% of the total variation in population characteristics is due to variability on the small scale. Part of this variation is undoubtedly caused by sampling, extraction and enumeration errors, but much of it is caused by the nature of the nematode populations themselves. The extraction method may only have recovered about 50% of the animals within a sample but the proportion was fairly constant. The sub-sampling method was generally reliable to within about 10% of the actual density of nematodes extracted from the sample. Hence the importance of the actual changes in the populations are probably somewhat less than 35%, however, small scale processes remain a major influence on population characteristics.

On the small scale stochastic processes appear most important. That stochasticism is a genuine characteristic of the populations and not an artifact of the procedures is shown by the fact that some species are very abundant and totally absent in adjacent, replicate samples (Appendix 1). Other species occur at very different densities in adjacent samples, too disparate to be explained by sampling errors alone. The absence of any distinct patterns in the population characteristics on this scale suggests that deterministic processes are not involved.

The absence of patterns could be caused by many different factors acting independently on single species (or small groups of species) so that the characteristics of the total population display no clear patterns. To positively ascertain whether this is happening requires detailed study of individual species, however it seems unlikely. The species examined in the dispersal experiment formed no patterns at all (section 4.2) and in the field, there were no strong influences on any of the most prominent species on the small scale. Hence the influence of small scale factors seems unlikely to be strong on any individual species.

The importance of stochastic processes is not surprising considering the multitude of spatially and temporally unpredictable factors on this scale - crab holes, mangroves leaves, roots and pneumatophores, microtopography, animal remains, algal blooms, even researchers and fishermen's footprints (section 1.3). Because these factors are so unpredictable on the small scale, the species which actually exploit favourable conditions in any or all of these factors may also be unpredictable. Hence if several species are all favoured by an ephemeral algal bloom then none, one, several, or all species may be able to exploit it, depending on chance. Such a mode of life has considerable implications for the biology of the nematodes (section 6.2.2)

The pattern of movement observed in the experiment (section 4.2) is also consistent with the stochastic hypothesis. If dispersal in the field is similar, it is slow enough to allow considerable heterogeneity in both space and time without being extensive enough to constantly mix the populations. However, it is not so slow that no changes in populations occur. The fairly constant slow dispersal should allow for some colonisation of new patches of suitable habitat but still leave a considerable element of chance in the occurrence of each species.

This small scale variation may be related to the mangrove trees. The sites which had the least small scale population changes were sites 12 and the Clyde River, both with only very small mangroves present. However, site 10 with no mangroves at all had quite variable populations and site 11, with mangroves, was quite uniform although this apparent uniformity probably resulted from the very low densities of nematodes found at this site. The nematode populations in the present study seem much more variable than those in European mud flats and also North American salt marshes (compare the species/abundance data in Appendix I with that of Warwick and Price (1979)).

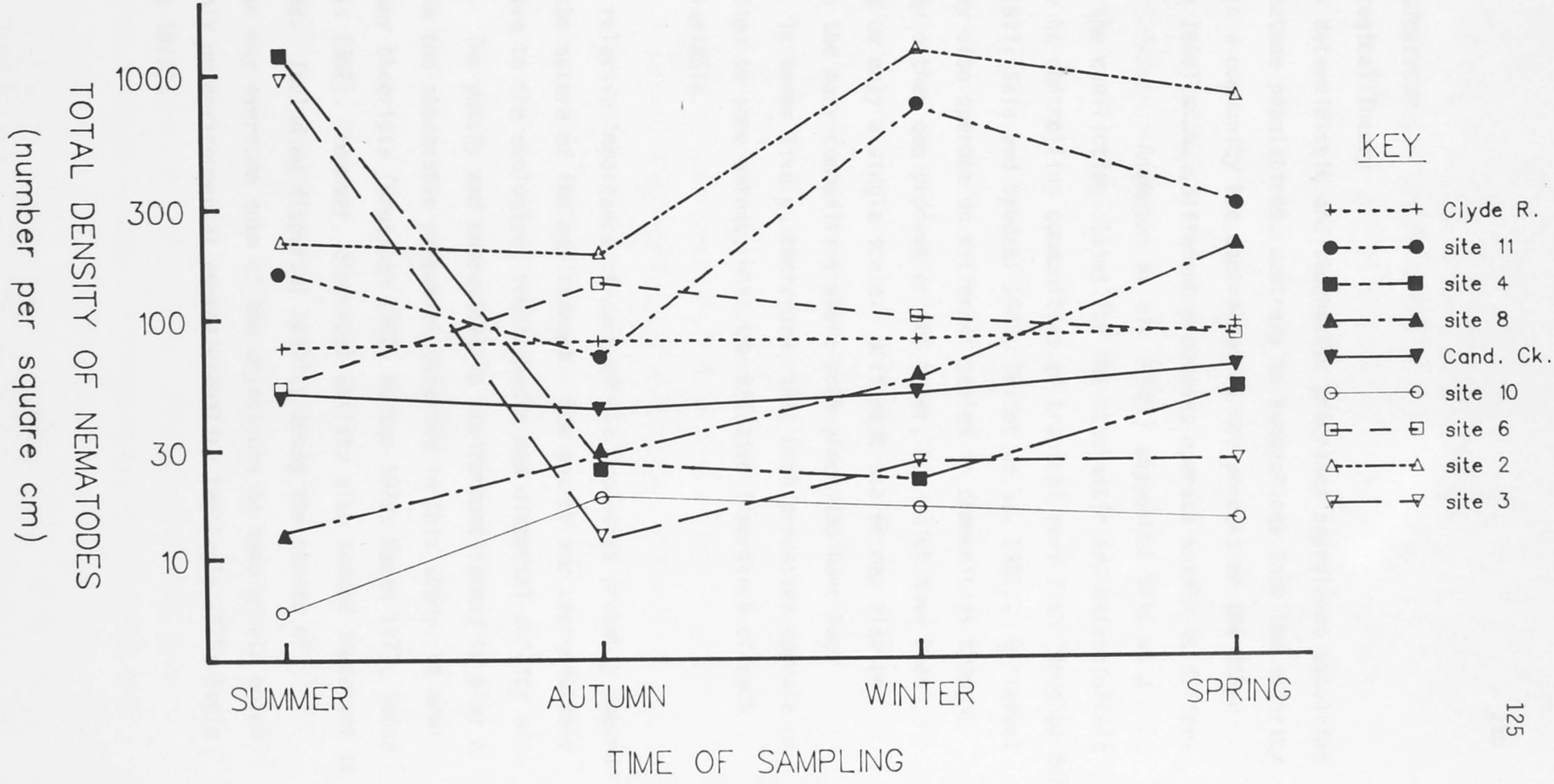
6.1.5 Temporal Change

About 8% of the total population variability is related to the time at which samples are taken, irrespective of the site. A further 20% is related to the site as well as time. What these temporal changes represent cannot be ascertained without data from more than one year, although some hypotheses can be offered.

The temporal variation which is uniform over all sites may represent either recurrent seasonal changes or the effect of some non-seasonal factor affecting all the sites, for instance rainfall or floods. Seasonal change seems more likely since the Clyde River and Candlagan Creek were sampled in a different year to the Hunter River and are less likely to be influenced by the same rainfall or flooding, etc. Whatever the cause, this temporal change probably involves species composition, since the total nematode population density does not change uniformly over the year (Figure 6.2), the other main possibility. The 25 species which are found at all sites provide ample scope for changes in species composition over time. No patterns in any of these species are immediately apparent from inspection of the complete table of species densities but a subtle pattern could have been overlooked because this source of variation is not very important.

The larger portion of temporal variation which differed among the sites, has already been allocated to medium scale variation because much of it is probably due to the nature of the sites (section 6.1.3). Part of this portion of the population variation is probably sampling inaccuracies and part the effect of the small scale stochastic processes. These are not the sole causes, however, because too much variance and too many important principal co-ordinates are involved. Indeed, because the sites have distinctive population characteristics, any seasonal changes will be different at each site.

FIGURE 6.2 TOTAL DENSITY OF NEMATODES IN ALL SAMPLES BY SEASON



6.2 *IMPLICATIONS*

6.2.1 Ecological Theory

Both deterministic and stochastic processes operate on estuarine littoral nematode populations, contrary to suggestions that the majority of species in a community are controlled by one process or the other (eg Grossman 1982). However, the different processes operate mainly at different scales. Anderson *et al.* (1981) suggested this as a solution to the conflicting claims for the stochastic and deterministic processes to be controlling communities of tropical reef fish (Roughgarden 1977; Sale 1977; Sale and Dybdahl 1975; Talbot *et al.* 1981). Different processes may also operate on different scales in communities thought controlled by either one process or the other, but which have been investigated on only a single scale. Different scales may also be important in the many communities where both processes have been implicated. It seems likely, therefore, that both processes operate on all communities to some extent, with the relative importance of each being very variable.

The relative importance of each of the processes probably depends largely on the nature of the environment - how patchy and unpredictable it is relative to the ecological requirements and dispersal ability of the animals. The patchy and unpredictable environment seemed to play a major role in the stochastic processes observed in this study, as predicted by many theorists (Grossman 1982; Huston 1979; Osman 1977; Sousa 1979a; Yodzis 1982). However, dispersal ability also seemed important is mangrove muds. Including dispersal ability among the causes of stochasticism may overcome some of the objections to some models which are based only on environmental unpredictability (eg Eagle 1975; Eagle and Hardiman 1977).

6.2.2 Biology of Estuarine Nematodes

The importance of stochastic processes and the quite dynamic model of the populations on the small scale, has considerable implications for the biology of the animals. Small scale stochastic variation in populations must be a considerable evolutionary force on nematodes. Stochastic processes favour dispersal ability and adaptability rather than specialisation because the environment is unpredictable. There is also little competitive pressure to specialise since the same species are not often in contact.

The restricted dispersal of the nematodes in this study is probably explained by morphological and size constraints on the musculo-locomotory system (Nicholas 1984). These constraints on dispersal emphasises the importance of adaptability. Adaptability may explain the distribution of many species and the numerous species from the same genus or closely related genera which coexist without any great divergence. Co-occuring species of such genera naturally have similar ecological niches but overlapping requirements do not necessarily mean that competition must be strong if the ranges of both species are broad. In any case, in populations controlled by stochastic processes the assumptions of the competitive exclusion principle are violated. This is thought to be common in a range of different animals and situations (Auclair and Goff 1971; Grubb 1977; Hebert 1974a, b; Loucks 1970; Weins 1977).

Lack of competitive pressure does not imply that the nematodes have not evolved adaptations to the estuarine environment. Clearly, the environment has had a considerable influence. However, lack of competitive pressure does imply that the specialised adaptations are more likely to directed towards larger scale environmental factors, such as oxygen availability and grain size.

6.3 *PRESENT LIMITATIONS AND FUTURE PROSPECTS*

6.3.1 Study Limitations

This study was necessarily a preliminary and exploratory investigation since, at the beginning, so little was known to science about nematodes from mangrove muds and the processes which control their distribution. Because of this, there are limitations and qualifications to the results. The study mostly considered only the charactersitics of the population as a whole rather than individual species, so some species may be influenced by factors other than those emphasised for the prominent species which dominated total population characteristics. Considering the total population has advantages, however, in determining which are the most important factors for the most important species without first having to determine which are the important species. Biological interactions among the species can also be investigated unlike in single species studies.

The results of this study apply only to spatial and temporal scales close to the sample size and interval. There may be many other influences and scales of change affecting estuarine littoral nematodes but nothing can be said about them from this study. Like all studies of this type, the sampling scales were influenced by initial preconceptions of what is likely to be important. However, a strength of this study must be that there were few preconceptions because marine nematodes are so cryptic and so little was known initially. The comparison of the different sampling scales should also have meant that the initial choice of the sample scale did not have an overwhelming impact on the results obtained.

There are philosophical and statistical problems in finding no pattern in a set of data. It is very difficult to test for randomness statistically, especially if the data has an unusual statistical distribution as it does here. In the absence of a test to prove that data are random, one must rely on the absence of patterns. However, no matter

how many samples were taken or how statistically efficient the methods of analysis, the criticism remains that more sampling or better analysis may have detected a pattern. All that can be said in answer to this criticism is that what evidence was available (Chapter 2) suggested that the sampling should have been extensive enough to detect any patterns and that the statistical methods are very sensitive and widely regarded as the best available (Appendix 3).

6.3.2 The Future

A practical result of this study is that it enables recommendations to be made about future sampling and analysis. The first is that considerable replication of sampling is necessary to distinguish between changes in populations on different scales. The second is that generally, the presence or absence of species is not a good indicator of the nature of a site or sample. One must consider the density or at least relative abundance of species if, as hypothesised here, the species fall into four (or more) ecological groups because the relative importance of the groups is most important, not their presence or absence. Third, ordination more clearly identifies the complex relationships between sites and species than cluster analysis. The specific details of recommended methods are in Appendix 3.

Now that the efficiency of sampling procedures, the importance of different scales and hypotheses of the main influences and processes affecting estuarine littoral nematodes have been established more intensive study is necessary. Of interest are the distributions of individual species, particularly those in the widespread fourth ecological group, with respect to the factors identified as important to the most prominent species. More comprehensive environmental measurements, including how the environment changes are important to test if other not measured here are involved, especially on the small scale. Direct tests of the influence of the various factors emphasised here on populations would be

fruitful in observing the mechanisms by which the population characteristics are affected. The development of a more realistic experimental system would allow this. Repetition of the present experiments in such a system may be useful.

Sampling on a scale smaller still than that considered here would be useful in giving an estimate of the variability within samples, as well as intrinsically interesting to see if there are other scales important to nematode populations. Further sampling on the large scale in other estuaries, especially more distant ones could confirm the generality of the patterns and processes found in this study.

6.4 *CONCLUSION*

This study suggests the following answers to its objectives (section 1.5):

(i) about 50% of the variability in population characteristics among samples represented deterministic patterns and about 35% represented stochastic variation (the origin of the remaining variation could not be ascertained);

(ii) the deterministic processes operated on the medium scale between different sites and the stochastic processes operated on the small scale between individual samples (a small amount of variation also occurred on the large scale between the different estuaries);

(iii) the deterministic patterns were caused by the grain size and redox potential of the sediment and the distribution of surface algae;

(iv) the environmental factors above affect three main ecological groups of nematodes directly rather than through interspecific competition;

(v) the pattern of dispersal observed in laboratory experiments was consistent with the hypothesis of stochastic processes controlling nematode population characteristics on the small scale.

The view of estuarine littoral nematode populations formulated here is loosely ordered and complexly patterned. These animals are affected by a number of different environmental factors on several different scales and live in diverse and dynamic populations. I make no apology for this complexity, because Whittaker (1952) and Gouch (1982) point out that ecological reality is loosely ordered and complexly patterned. Apart from the intrinsic interest in these largely neglected animals as part of the important estuarine system, this study has shown their utility as a model for general ecological theory. This study is a start, providing a little information and many hypotheses for future work. The intertidal mud of estuaries is not lifeless as may first appear but a dynamic *terra incognita* awaiting more exploration.

APPENDIX 1:

DISTRIBUTION OF NEMATODES IN THE SAMPLES

Tables A1.1 and A1.2 show representative portions of the data of species densities per cm^2 analysed in this thesis. The full data of the densities of the 89 species in the 180 samples are available as a computer data file. However, the portions shown illustrate the salient features of the data -

* the large number of zero density records,
* the great variation in species densities when present, even among replicate samples,
* the very high densities of some species,
* the densities of some species are bimodal and do not fit the Normal, Binomial, or Poisson distributions.

Note that one of the samples was lost (Ca II E). For the purposes of analysis this sample was taken to have exactly the same population characteristics as the adjacent sample (Ca II D). This approximation of the fauna has no effect on the relationships found amongst the other samples by cluster analysis and should have little effect on the other analyses.

TABLE A1.1 Density of some of the nematode species at site 11 (number per cm^2)

SPECIES	SAMPLE 11 I A	11 I B	11 I C	11 I D	11 I E	11 II A	11 II B	11 II C	11 II D	11 II E
Terschellingia longicaudata	.6	.0	.2	.0	.8	.0	.3	.2	.1	.0
Terschellingia sp. B	.6	.0	.0	.0	.2	.0	.0	.0	.0	.0
Metalinhomoeus sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Spirinia sp.	.0	.0	.0	.6	.0	.0	.0	.0	.0	.0
Onyx sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Terschellingia sp. C	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Xyala sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sphaerolaimus sp. A	.2	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sphaerolaimus sp. B	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sphaerolaimus sp. C	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sabatieria sp.	.4	.0	.0	.2	.4	1.4	6.7	1.0	2.5	2.3
Laimella sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Alaimella sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Vasostoma sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Calyptronema sp.	.0	.0	.0	.6	.0	.0	.0	.0	.0	.3
Phanoderma sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Desmodora sp. A	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Desmodora cazca	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Anoplostoma sp.	1.2	.0	.0	.0	.0	.0	.6	.7	.2	.0
Chaetonema sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Tripyloides sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0

SPECIES	SAMPLE 11 III A	11 III B	11 III C	11 III D	11 III E	11 IV A	11 IV B	11 IV C	11 IV D	11 IV E
Terschellingia longicaudata	.2	.3	.4	.0	.1	.0	.0	.2	.0	.0
Terschellingia sp. B	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Metalinhomoeus sp.	.0	.6	.1	.3	.0	.0	.3	.0	.0	.0
Spirinia sp.	.1	.0	.0	.0	.0	.2	.0	.1	.0	.0
Onyx sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Terschellingia sp. C	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Xyala sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sphaerolaimus sp. A	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sphaerolaimus sp. B	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sphaerolaimus sp. C	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sabatieria sp.	.2	8.2	.5	2.9	.5	.1	.0	.0	.0	.0
Laimella sp.	.2	.3	.1	2.0	.3	.0	.0	.0	.0	.0
Alaimella sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Vasostoma sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Calyptronema sp.	.2	.0	.1	.3	.0	.0	.0	.0	.0	.2
Phanoderma sp.	.0	.0	.0	.0	.0	.0	.0	.0	.1	.0
Desmodora sp. A	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Desmodora cazca	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Anoplostoma sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Chaetonema sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Tripyloides sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0

TABLE A1.2 Density of some of the nematode species at site 2 (number per cm^2)

SPECIES	SAMPLE 2 I A	2 I B	2 I C	2 I D	2 I E	2 II A	2 II B	2 II C	2 II D	2 II E
Terschellingia longicaudata	9.8	1.4	4.1	.0	.0	.0	.8	5.7	.0	.0
Terschellingia sp. B	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Metalinhomoeus sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Spirinia sp.	11.4	4.1	4.1	1.5	.0	.8	3.2	.0	1.5	.0
Onyx sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Terschellingia sp. C	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Xyala sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sphaerolaimus sp. A	14.7	11.0	22.4	10.2	21.2	8.0	3.2	31.4	4.4	16.0
Sphaerolaimus sp. B	.0	.0	4.1	1.5	3.3	.0	.0	.0	.0	.0
Sphaerolaimus sp. C	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sabatieria sp.	29.3	11.0	12.2	26.2	21.2	3.2	56.0	22.9	10.2	6.4
Laimella sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Alaimella sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Vasostoma sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Calyptronema sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Phanoderma sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Desmodora sp. A	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Desmodora cazca	8.1	42.8	40.7	13.1	26.1	2.4	1.6	8.6	13.1	19.2
Anoplostoma sp.	6.5	.0	.0	1.5	.0	.0	.0	.0	.0	3.2
Chaetonema sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Tripyloides sp.	6.5	11.0	18.3	13.1	14.7	56.8	9.6	168.6	88.7	210.9

	SAMPLE 2 III A	2 III B	2 III C	2 III D	2 III E	2 IV A	2 IV B	2 IV C	2 IV D	2 IV E
Terschellingia longicaudata	.0	.0	.0	.0	.0	1.9	1.3	2.7	2.6	1.1
Terschellingia sp. B	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Metalinhomoeus sp.	.0	.0	.0	.0	.0	.6	.0	.5	.0	.0
Spirinia sp.	3.5	.0	32.3	.0	21.7	4.4	1.3	1.1	4.3	3.2
Onyx sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Terschellingia sp. C	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Xyala sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sphaerolaimus sp. A	.0	42.7	64.5	10.9	76.1	.0	.0	.5	2.6	.5
Sphaerolaimus sp. B	.0	.0	.0	.0	.0	.0	1.3	.0	.0	.0
Sphaerolaimus sp. C	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Sabatieria sp.	.0	12.2	64.5	76.1	43.5	12.1	11.8	12.3	7.8	25.6
Laimella sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Alaimella sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Vasostoma sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Calyptronema sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Phanoderma sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Desmodora sp. A	.0	.0	.0	10.9	.0	.0	.0	.0	.0	.0
Desmodora cazca	112.9	61.0	483.9	130.4	97.8	2.5	31.5	3.7	34.8	.5
Anoplostoma sp.	.0	.0	.0	.0	.0	.0	1.3	.0	.9	.0
Chaetonema sp.	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
Tripyloides sp.	.0	420.7	2322.6	782.6	673.9	.0	.0	.0	.0	.0

APPENDIX 2:

EXTRACTION METHOD

Nematodes were extracted from sediment samples by a combination of sedimentation, sieving and centrifugation as detailed by Hodda and Nicholas (1985). The sample was stirred vigorously in a large volume of tap water and then passed through a 2 mm mesh sieve to remove large particles. The filtrate was stirred again, then allowed to settle for 1 minute in a 1 litre measuring cylinder (to remove sand grains), then passed through a 50 μm mesh sieve to collect the nematodes together with other fine particulate material. This was repeated with 40 and 20 seconds settling time. The residue was washed from the filter and further separation carried out by centrifugal filtration.

A spoonful of kaolin was added to the suspension, which was then shaken up and centrifuged for 7 minutes at about 300 radians per second. The supernatant was discarded and the pellet resuspended in 30 ml of colloidal silica (Ludox, Du Pont de Nemours, Delaware, USA) with a specific gravity of 1.15. After re-centrifugation for 7 minutes at 300 radians per second, the supernatant was again collected on a 50 μm nylon sieve and washed into a petri dish with water. The proportion of the sample containing about 100 nematodes was estimated, the sample rehomogenised in a small vial and the proportion containing 100 nematodes returned to the petri dish. This subsample was gradually transferred to anhydrous glycerol from a 5% (v/v) solution and the nematodes mounted on microscope slides.

APPENDIX 3:

STATISTICAL METHODS

The following discussion is not intended as an extensive critique of the various methods of analysis available. It is merely a discussion of why I used the methods I did, and why I didn't use some of the other methods proposed.

a) **General**

In largely exploratory studies such as this, one must collect large amounts of data from which to generate hypotheses. The best way to handle such data objectively is by multivariate analysis. Multivariate analyses generally require no null hypothesis as do classical statistics. They are also much stronger when dealing with many variables. Multivariate statistics also do not require random sampling locations - very difficult when thigh deep in mud or in vast, featureless mangrove forests.

Multivariate analysis does have potential pitfalls, however. There are many methods available, most developed quite recently and one must avoid choosing the method of analysis to fit preconceptions of the results. In particular, the statistical properties of the data should match any assumptions as well as any strengths and weaknesses of the method chosen. The method should also be robust to small changes in the data, such as those which may arise due to the vagaries of sampling. Small changes in the data should produce only small changes in the results, not large ones. Gauch (1983) discusses the strengths, problems and philosophy of multivariate analysis in more detail.

The only real alternative to multivariate methods in exploring the importance of different scales of change in complex population data is Green's Index of Dispersion (Green 1966). This method relies on taking replicate samples of several different sizes and comparing the

ratio of the variance in density between replicates to the mean density for each sample size. The sample size with the greatest ratio indicates the scale which animals are aggregated and the value indicates the degree of aggregation. This method has one advantage over my methods in that the only initial decision required is the choice of sample size, which is relatively minor since a range must be chosen anyway. My methods required initial choice of both the basic sample size and the location of different sites for sampling on the larger scales. In practice this is not a serious problem since the larger scales of sites and estuaries are, on the whole, observably different and discrete from surrounding areas. Also, because nematodes cannot be directly observed in the field, preconceptions of patterns in the nematode fauna can be discounted.

Green's Index has many disadvantages. There are no tests for the significance of difference in the index and no indications to the cause of aggregation, although the scale may provide clues. The method is limited to a narrow range of small core sizes because of physical constraints in taking comparable samples of different sizes and time constrains in counting animals from very large samples. Several small samples, in any case, contain all the information of a single large sample, plus the information about the smaller scale as well. This has been demonstrated in this study. The final objection to Green's Index, as applied to nematodes is that it relies on the mean and variance of density, which are difficult to quantify because nematode densities in this study were not normally distributed (Appendix 1).

b) **Ordination Methods**

Of the many ordination methods available, Principal Co-ordinate Analysis was used initially in this study because it requires few assumptions and is very general. Principal Co-ordinate Analysis starts with a table of all the pairwise comparisons of site similarity (a similarity matrix) rather than raw species/abundance data. This allows the choice from an

enormous range of similarity coefficients to measure the desired properties of the population under study without many restrictions on the statistical distribution of the original data. (Similarity indices are discussed further in Appendix 3d). A disadvantage of starting with a similarity matrix is that principal co-ordinates cannot be directly related to the individual species and one cannot tell which species are most important in the patterns identified on a particular axis.

Because of this limitation the relationships among the distributions of the different species had to be examined separately (section 5.2). Principal Component Analysis was used rather than Principal Co-ordinates because the data in this case were the total densities of each species at each site, obtained by summing the densities in the samples. This meant that there were much fewer 0 density records (29% as against about 68% in the individual samples) and that the statistical distribution of the species densities was closer to a normal distribution with less extreme variations than in individual sample densities. Under these conditions, Principal Components Analysis is more powerful than Principal Co-ordinate Analysis, because it retains the original data about individual species.

In this study Principal Components Analysis was performed on a dispersion matrix rather than the correlation matrix. The dispersion matrix of variances and covariances of the species is based on the raw data so that the densities of the different species is taken into account. A correlation matrix, however, standardises all species densities to be equal, which would give very rare species inordinate influence.

A number of different graphic forms are used in this thesis to represent individual principal co-ordinates/components, including points in 3-dimensional space. Both principle co-ordinates and components are, however, vectors. This makes no difference to the interpretation of the

various graphs where other representations are used for greater clarity, however, it is noted here for completeness. That both ordination techniques used operate on vectors rather than points explains why principak co-ordinates (and components) near zero have little mathematical meaning and are not included on many graphs.

Most other important features of Principal Co-ordinate and Principal Component Analyses were described in section 2.2. The mathematical procedures, as developed by Gower (1966) and Hotelling (1933) respectively, are described in a number of texts (eg. Legendre and Legendre 1983) and so will not be described again here.

Principal Co-ordinate and Component Analyses have, to my knowledge, not been applied to nematode populations before. The only authors to consider nematode populations in any similar way were Ferris, Ferris, Bernard and Probst (1971) and Johnson, Ferris and Ferris (1973, 1974). Both groups used an ordination method from plant ecology (Bray and Curtis 1957) which required *a priori* choice of reference sites according to what seemed to be the most important species. The faunal characteristics of other sites were then related to the several reference sites. This method of ordination, as distinct from the Bray-Curtis similarity coefficient which is discussed in Appendix 3d, is less desirable than Principal Co-ordinate Analysis because it requires this initial choice of reference sites. It also allows only a few axes to be easily considered and gives no indication of the relative importance of the different ordination axes. It was also designed originally for hand computation and computer programs are no longer available since the much more mathematically desirable Principal Co-ordinate Analysis was developed.

c) **Cluster Analysis Methods**

By contrast with ordination, cluster analysis has been used in several studies on sub-littoral nematode populations, with some success (Johnson, Ferris and Ferris 1972; Tietjen 1976, 1977). Nevertheless, I took a fresh look at the clustering methods available.

Cluster analysis, like Principal Co-ordinate Analysis, begins with a similarity matrix but may then order the sites (or species) according to a range of criteria between two extremes (Williams *et al.* 1978). At one extreme, descriptive clustering aims to avoid misclassifying a site under any circumstances, even if clusters consist of only single sites. At the other extreme, synoptic clustering forces all sites into large clusters, irrespective of how tenuous the similarity. In this study the interest is in the similarity values between different clusters as well as the way sites are arranged, so an accurate representation of the relationships avoiding the distortion of either extreme, is required.

Group Average Sorting is the best method according to this criterion (Lance and Williams 1967a), and so was used in this study. This is the same method used by Tietjen (1976, 1977). It was found to best represent plausible relationships between samples from a preliminary survey small enough to examine without statistical aid. It also has theoretical advantages over other clustering methods. Single Linkage Clustering contracts the reference space, making it progressively easier to join a cluster of sites as it becomes larger (Lance and Williams 1967a) and Flexibile Clustering (with the usual value of $\beta=^{-}0.25$) also distorts the relationships among sites to produce a more attractive dendrogram (Legendre and Legendre 1983). Centroid Sorting is geometrically appealing but very often confusing in practice because of reversals - when the similarity of two groups of sites is greater than the similarity of their individual members. Centroid Sorting should also only be used for samples from random locations (Legendre and Legendre

1983). Information Analysis is a clustering method working on totally different principles to all the other methods mentioned but requires enormous computing resources (Lance and Williams 1967b; Williams, Lambert and Lance 1966). It operates only on presence or absence data and has problems dealing with joint absences. The clustering method used by Johnson *et al.* (1972) on nematodes is related to Information Analysis but little is known of its properties other than that it, too, is computationally awkward.

Mathetical details of the method can be found in many texts (eg Legendre and Legendre 1983).

d) **Similarity Coefficients**

The starting point for both cluster and Principal Co-ordinate Analyses is a matrix of the similarities between every pairwise combination of sites (or species). Hence the choice of a measure of the similarity in population characteristics between sites (or in the distributions of different species) is very important. A large number of similarity coefficients have been proposed - Lamont and Grant (1979) list 60 and Legendre and Legendre (1983) a number of others. (Similarity coefficient is used throughout this thesis as a comprehensive term for what should be strictly called similarity, dissimilarity, distance and association coefficients (Legendre and Legendre 1983).)

The Bray-Curtis similarity coefficient was chosen for comparing the population characteristics of the sites:

$$S_{(a.b)} = \frac{2W}{A + B}$$

where $S_{(x.y)}$ is the similarity between sites x and y, W is the sum of the lesser densities of each species at the sites and A + B is the sum of the total densities at each site. This coefficient was developed by

Steinhaus (Motyka *et al.* 1950), and came into wide use after an extensive study by Bray and Curtis (1957).

The Bray-Curtis similarity coefficient was used with some success by Tietjen (1976, 1977 and 1980) in studies on sub-littoral nematodes, although under a different (incorrect) name. In a comprehensive simulated trial, this coefficient best represented the true resemblance of different sites along the entire scale (Bloom 1981). It also gave the most plausible pattern of relationships among samples from a preliminary survey of the Hunter River which was small enough to compare the population characteristics of the sites by inspection. The Bray-Curtis coefficient is also recommended by Legendre and Legendre (1983) for use on raw abundance data which has not been transformed to approximate any standard statistical distribution. Transformation was undesirable in this study because it would change the patterns of variation in the data (see below and Chapter 2).

The only potential disadvantage of the Bray-Curtis similarity coefficient is that it is only a semi-metric. This means that it does not fulfil one of the mathematical axioms which a similarity coefficient must satisfy to be certain that the results of a Principal Co-ordinate Analysis are meaningful (Legendre and Legendre 1983; Sneath and Sokal 1973). In particular, it can result in principal co-ordinates which account for a meaningless negative proportion of the variance. However, this did not occur in any of the Principal Co-ordinate Analyses in this study (Figure 3.9; Tables 4.1 and 4.2; Appendix 4).

When there are many zero records in the table of species densities, as in this study, some authors recommend using a similarity coefficient which compares sites only according to the presence or absence of a species, not its density (Revelante, Williams and Bunt 1982). They claim that most of the information about population similarities resides in the presence/absence dichotomy, however the

densities of the different species vary so widely in my data that much of the information about the distribution of the important, very abundant species would be lost. The many species which occurred at very low densities dominated presence/absence similarity coeffients in the preliminary trials. Coefficients using presence/absence or percentage abundance data also deliberately eliminate much small scale variation (Gauch 1982). This is often desirable when identifying any pattern in the data is of primary concern, however this study requires an accurate representation of the data to determine how important any patterns are, as well as what a pattern represents. Williams, Clay & Bunt (1982) successfully used the Bray-Curtis similarity coefficient on species density data having 79% zeros, considerably more than the 68% in this study. The Bray-Curtis coefficient seems unaffected by data having large proportions of zeros because it ignores joint absences.

Problems with zero densities make most coefficients using distances between points unsuitable. Zero densities contribute inordinately to such coefficients (Legendre and Legendre 1983; Orloci 1979) and samples with no species in common can be regarded as more similar than samples which do share species (section 2.2). Using Euclidean distance as a measure of similarity between samples is undersirable because it is affected by the number of species present (Legendre and Legendre 1983). Proposed solutions to this problem have other undesirable properties. Using average densities eliminates the relative importance of the different species and standardises the great range of densities. Normalising the species densities is equivalent in theory to increasing the size of a sample by a indeterminate amount. This is undesirable here because the sample sizes are important. The problem with joint absences contributing inordinately to the similarity coefficient remains with many of the proposed modifications to Euclidean distance. The Manhattan metric coefficient has similar undesirable properties to Euclidean distance. The Czechanowski coefficient (equal to the Manhattan metric divided by the number of species) eliminates the

effect of the number of species present but the other problems with distance coefficients remain. The Canberra metric, in addition to the other undesirable properties, counts differences in the abundance of low density species relatively more than differences in species at higher densities. Gower's similarity co-efficient, which does handle joint absences well, was found a poor indicator of the relationships between samples in preliminary trials on a small data set.

Parametric coefficients of similarity, like the covariance of two sites or Pearson's R, require data at least approximating a normal distribution. However, normalising data changes its nature (above) and in this case would be difficult because of the unusual statistical distribution of the raw data (Appendix 2). Also, the undesirable influence of joint absences cannot be eliminated except by manually deleting all rare species from the calculations.

A final similarity coefficient considered was that of Preston (1962). This coefficient was used in studies of terrestrial nematodes by several investigators (Ferris *et al.* 1971; Johnson *et al.* 1972, 1973 and 1974). This coefficient is based on the log-series distribution empirically constructed by Preston (1962) and extrapolated to apply to all animals. The log-series distribution of species abundances has, however, no theoretical basis (Pielou 1975) and does not fit the present data well in any case.

APPENDIX 4

ANALYSIS OF INDIVIDUAL SITES

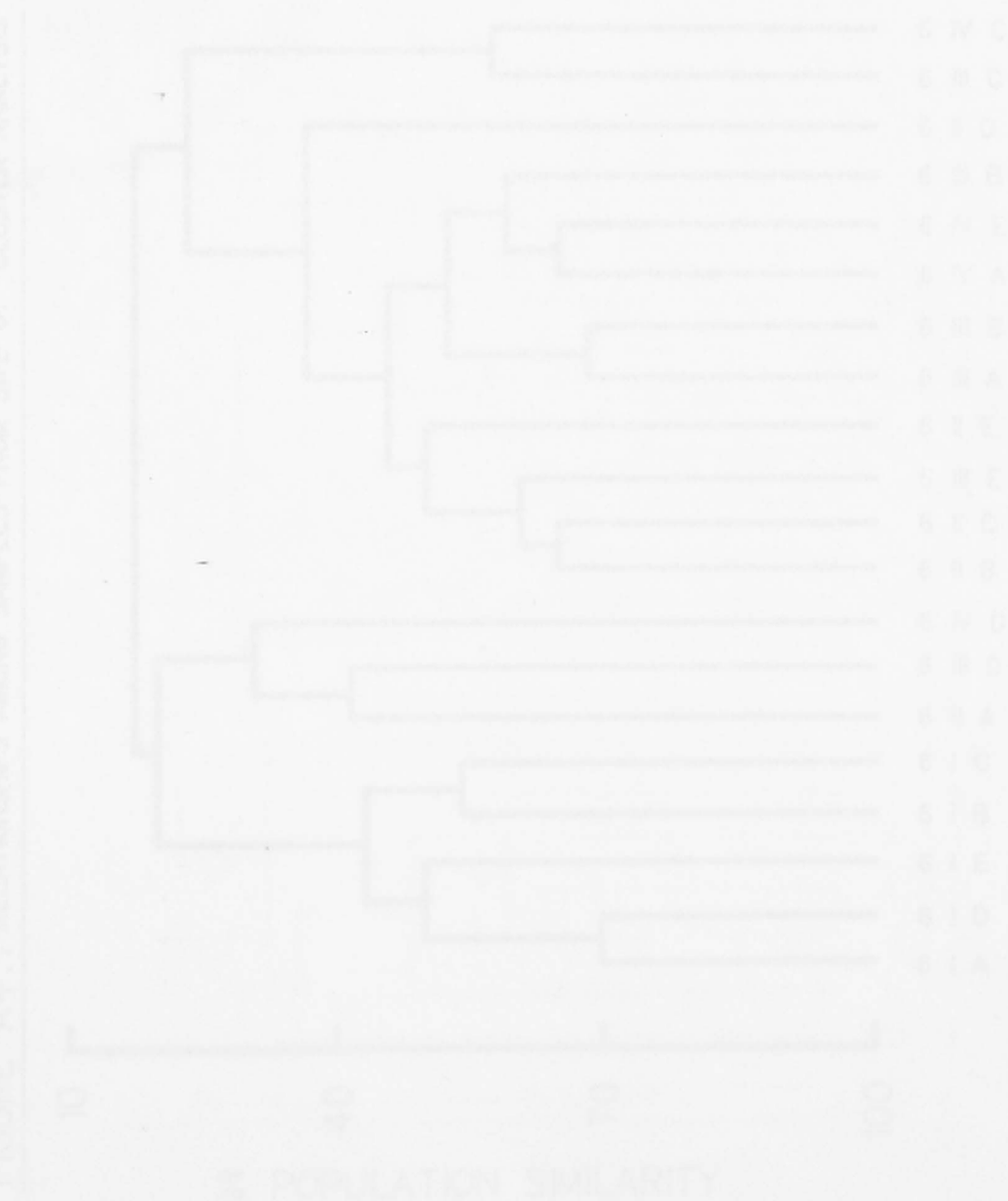


FIGURE A4.1 RELATIONSHIPS AMONG SAMPLES FROM SITE 6: CLUSTER ANALYSIS

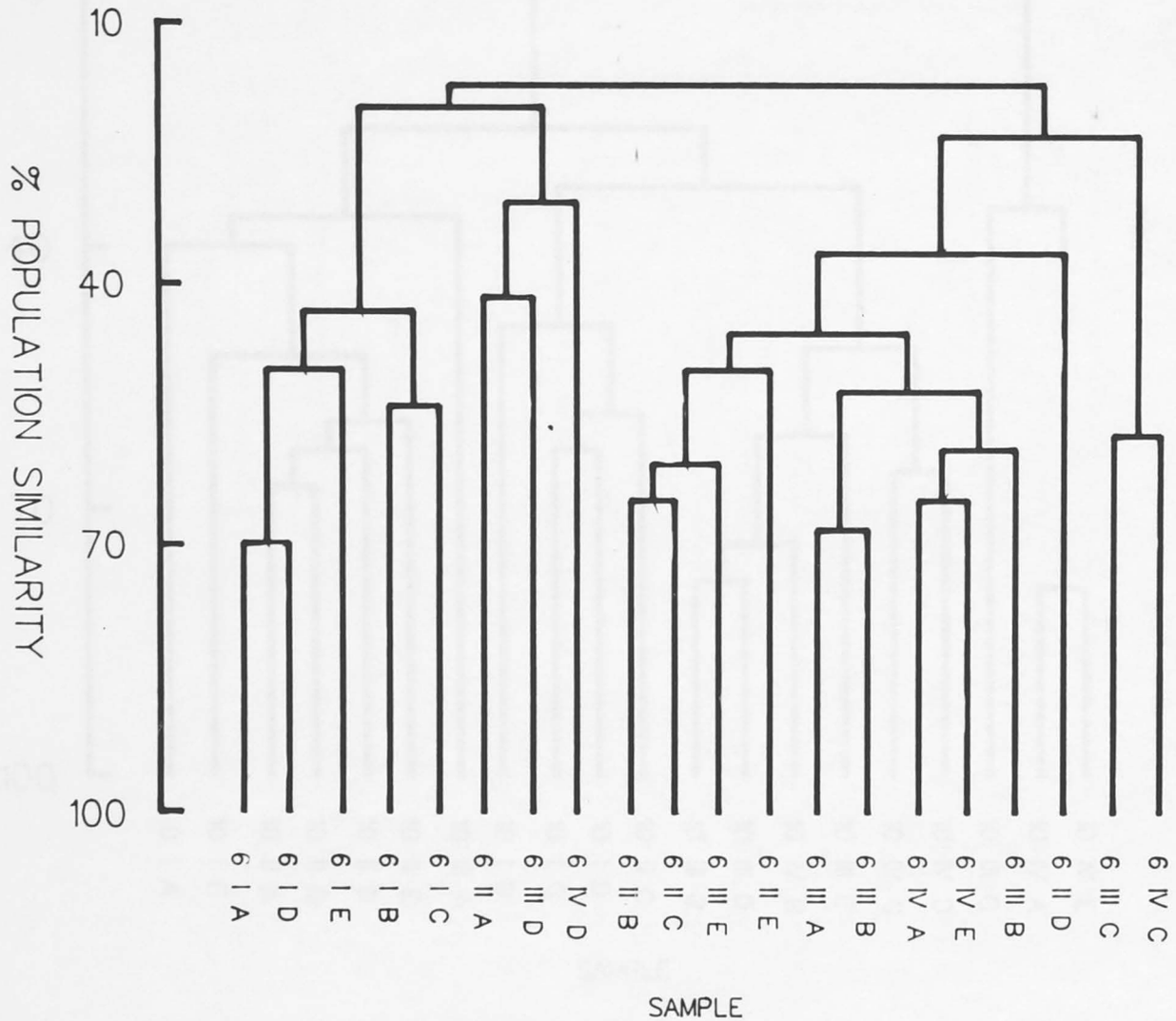


FIGURE A4.2 RELATIONSHIPS AMONG SAMPLES FROM SITE 10: CLUSTER ANALYSIS

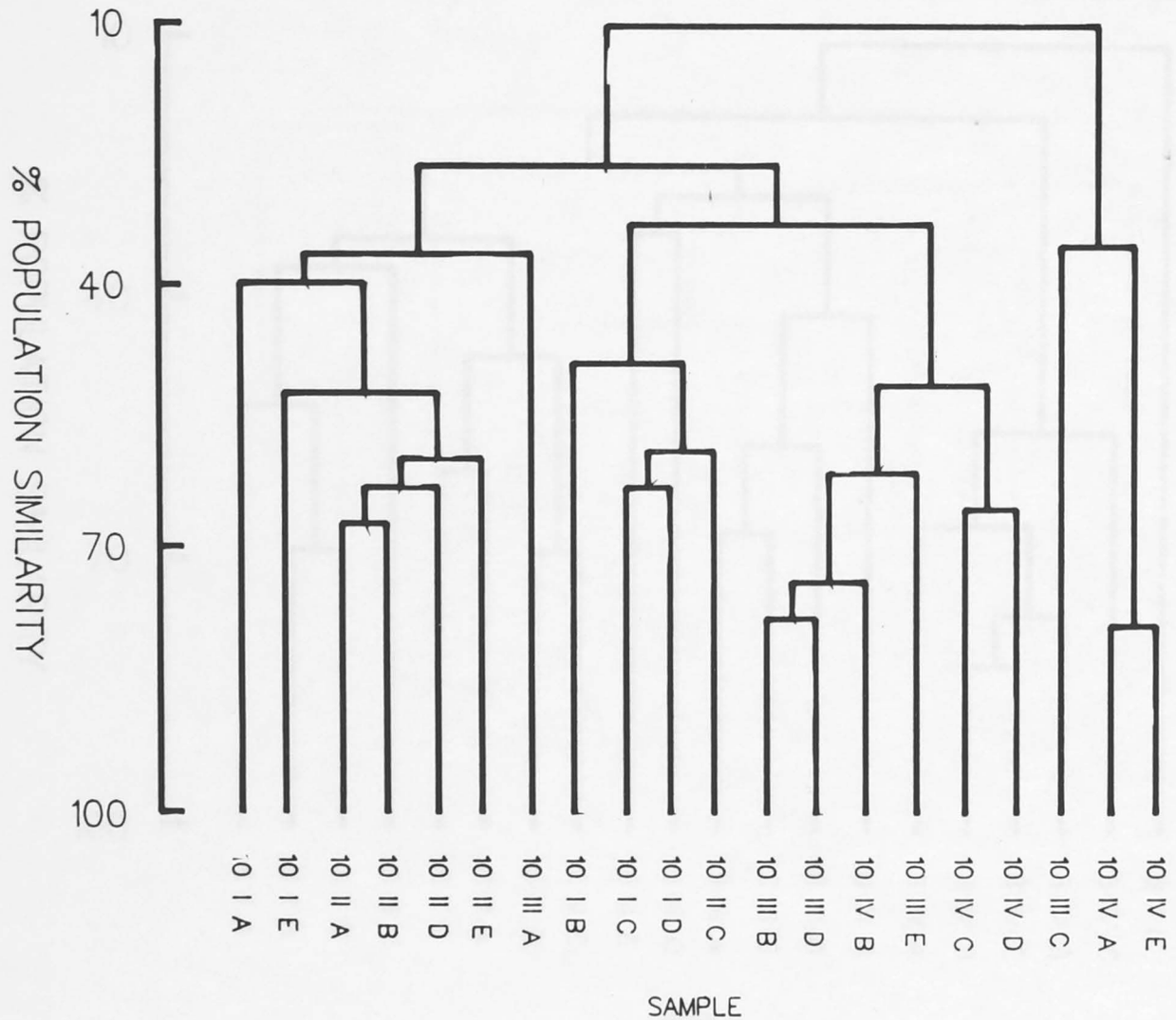


FIGURE A4.3 RELATIONSHIPS AMONG SAMPLES FROM SITE 8: CLUSTER ANALYSIS

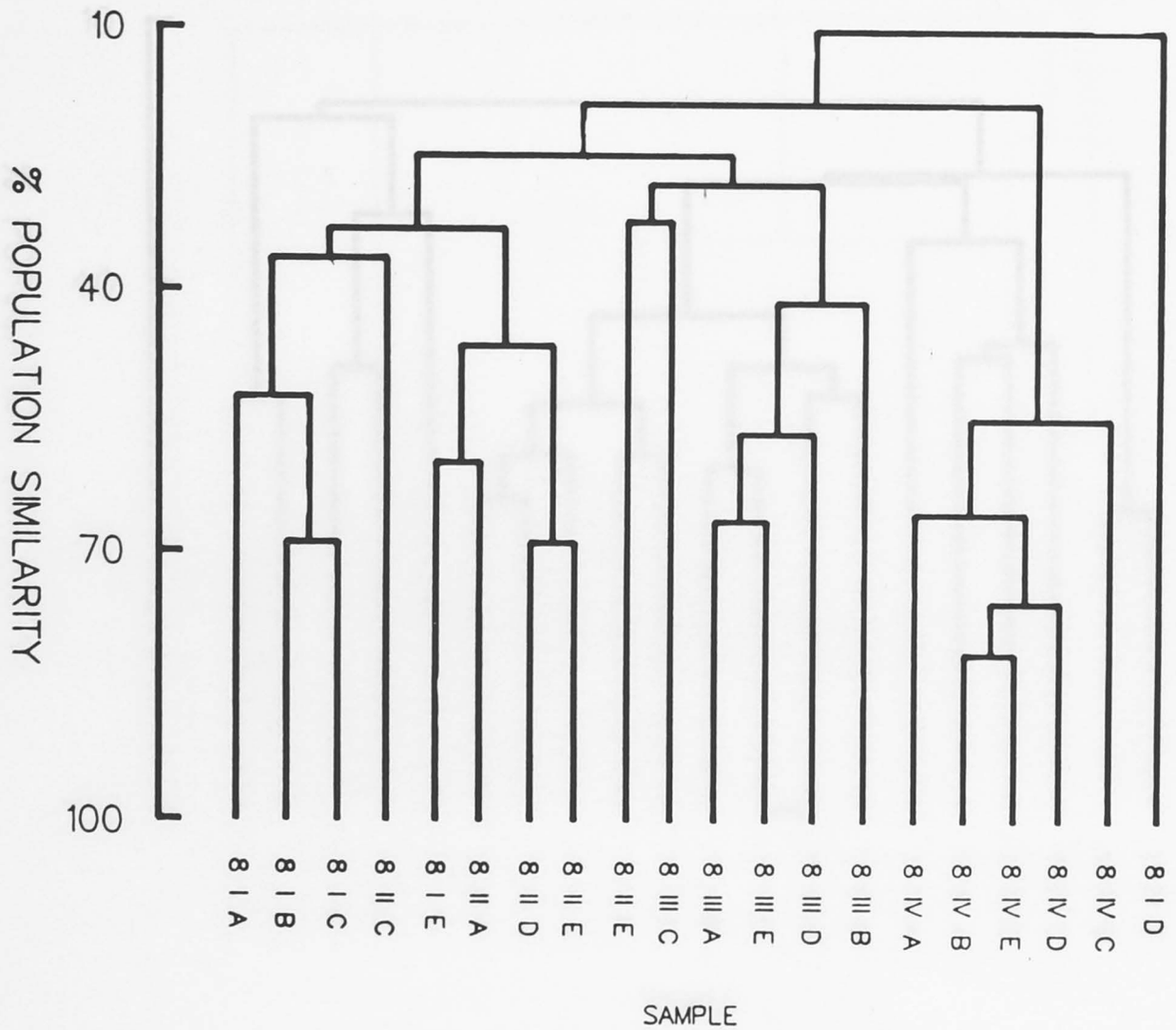


FIGURE A4.4 RELATIONSHIPS AMONG SAMPLES FROM SITE 11: CLUSTER ANALYSIS

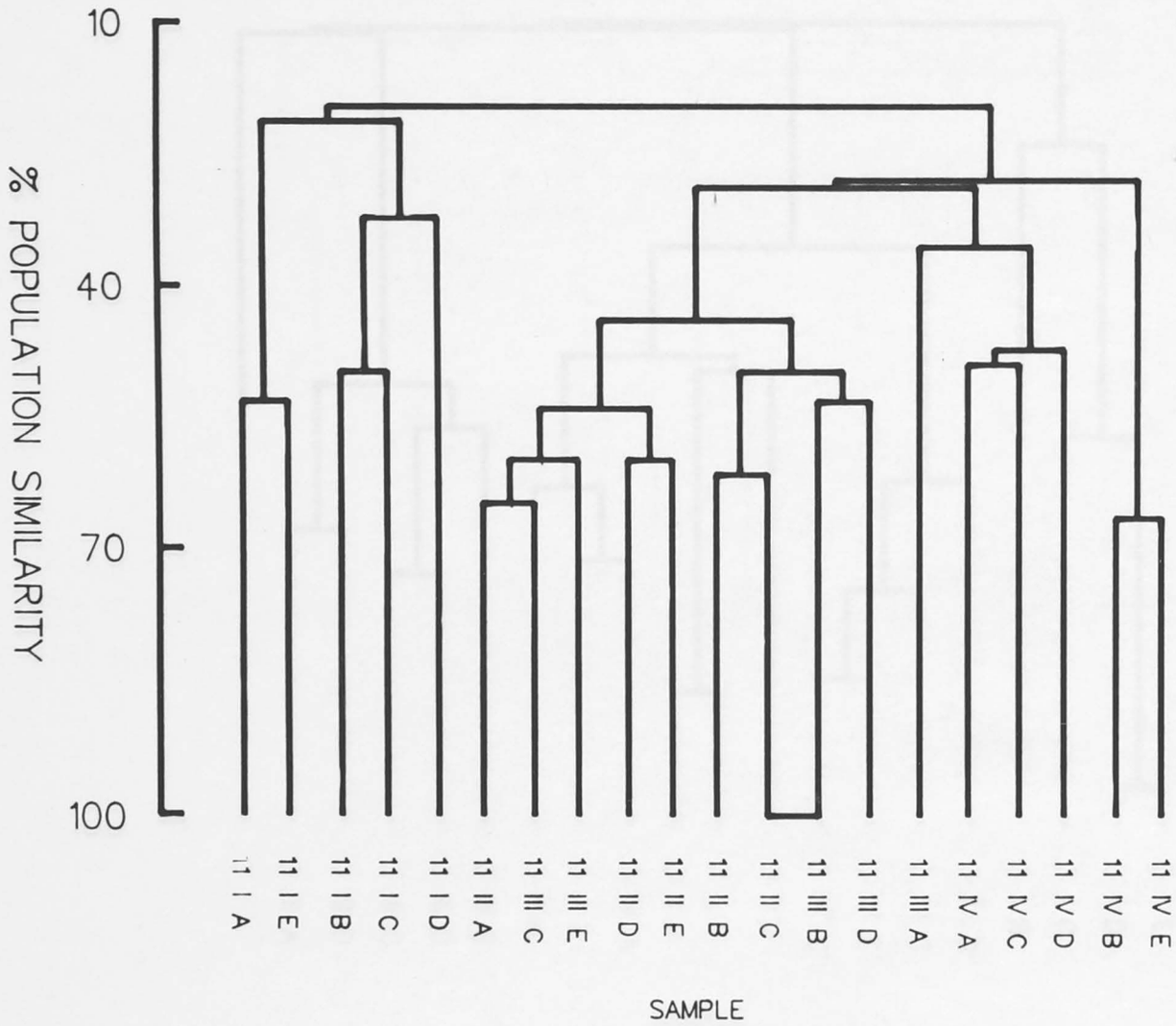


FIGURE A4.5 RELATIONSHIPS AMONG SAMPLES FROM SITE 3: CLUSTER ANALYSIS

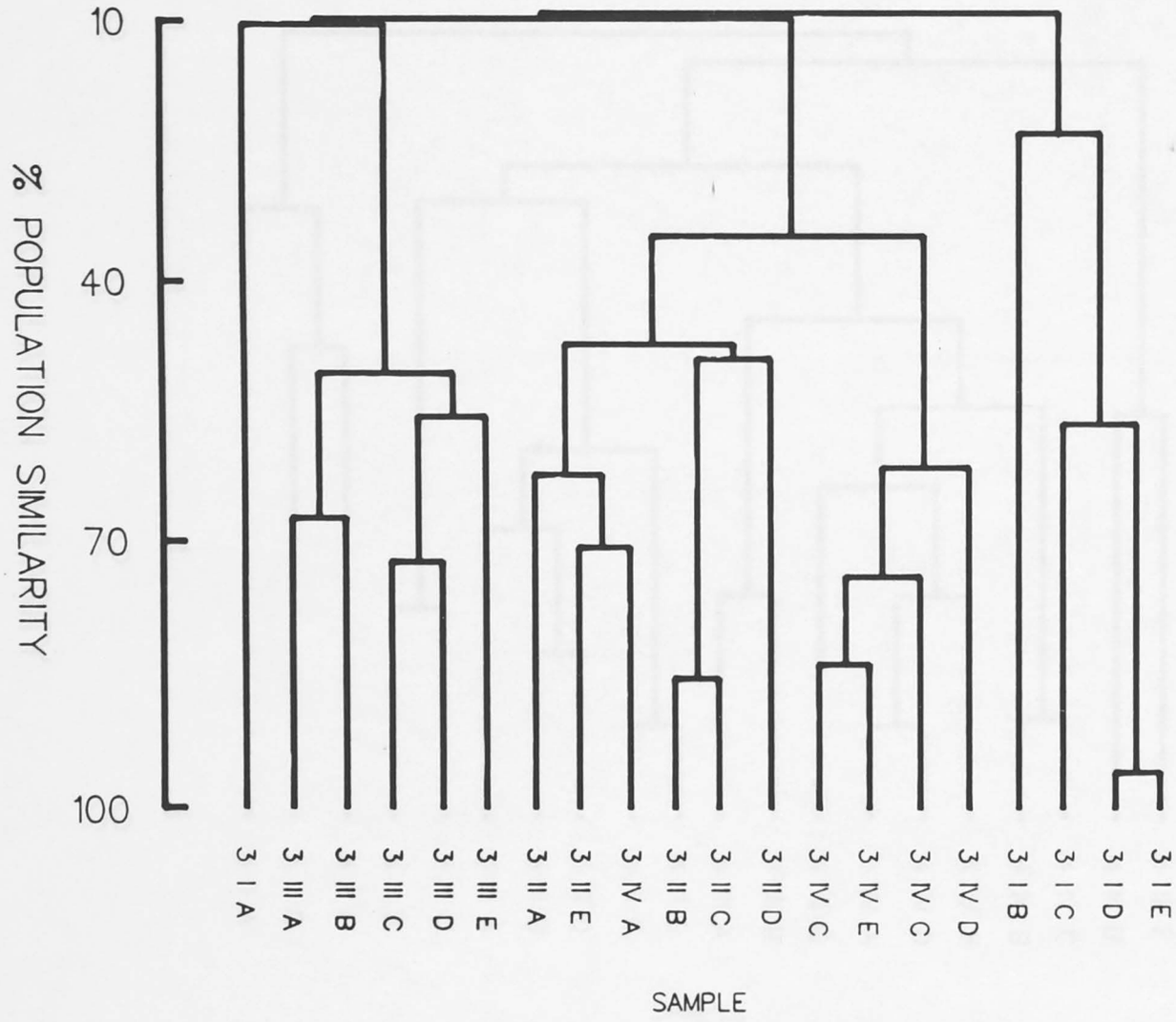


FIGURE A4.6 RELATIONSHIPS AMONG SAMPLES FROM SITE 4: CLUSTER ANALYSIS

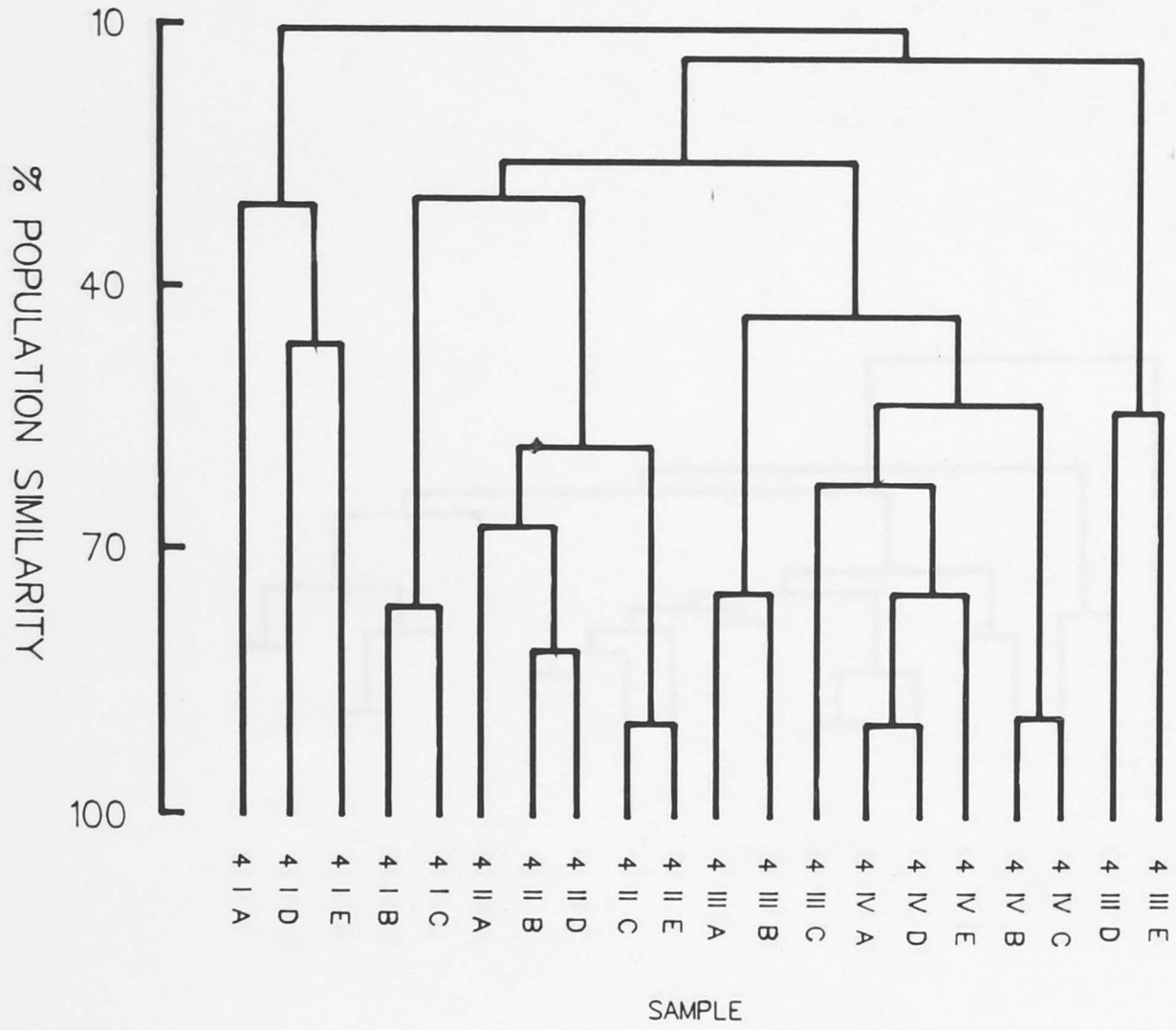
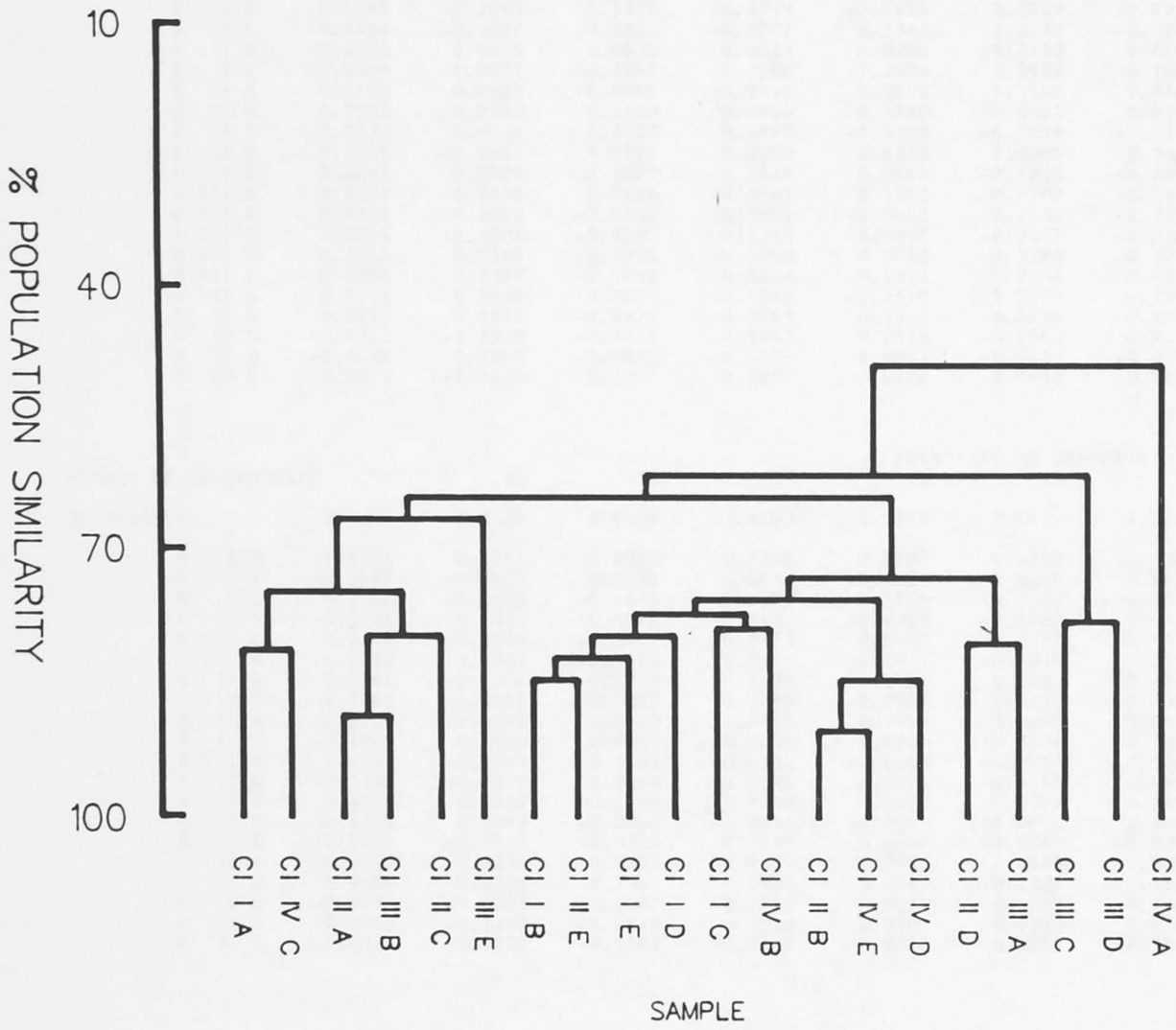


FIGURE A4.7 RELATIONSHIPS AMONG SAMPLES FROM CLYDE RIVER: CLUSTER ANALYSIS



PRINCIPAL CO-ORDINATE

NUMBER OF CO-ORDINATE			1	2	3	4	5	6	7	8	9	10
% VARIANCE			20.1122	11.5625	9.7088	7.2102	5.9096	5.5558	5.0581	4.2724	4.2055	4.0467
SAMPLE	6	I A	-0.5908	0.1260	0.1367	-0.0298	-0.0787	-0.2926	0.0632	0.0333	0.1008	0.1837
	6	I B	-0.5966	-0.2294	0.1322	-0.1099	-0.0616	0.2222	-0.0962	-0.0373	0.0960	0.1235
	6	I C	-0.4494	-0.3097	0.2211	0.0077	0.1342	0.3572	-0.3274	-0.0091	0.2397	-0.0143
	6	I D	-0.6158	0.2016	0.0638	-0.0524	-0.0266	-0.3722	0.0692	-0.0375	0.0746	0.0780
	6	I E	-0.6009	-0.0681	0.0287	-0.1788	-0.2875	0.0502	0.1683	0.1278	-0.4164	-0.2167
	6	II A	0.0220	0.4302	-0.0656	0.2715	0.0600	0.1556	0.0481	0.5461	0.1463	-0.2156
	6	II B	0.1639	0.0383	0.2493	0.4853	-0.1740	-0.0182	0.0250	-0.1195	-0.0353	-0.0584
	6	II C	0.2723	-0.0118	0.2222	0.3483	-0.1309	-0.0894	-0.0129	-0.0734	0.0256	0.0758
	6	II D	0.1686	-0.2641	0.2791	0.0282	0.5318	0.0005	0.4340	0.0875	-0.1200	0.1744
	6	II E	0.2005	-0.2729	0.2801	0.1512	0.0664	-0.0228	-0.2273	-0.1089	-0.3144	-0.2146
	6	III A	0.3891	-0.1418	0.0480	-0.2989	0.1365	-0.2508	-0.2488	0.1696	-0.0153	-0.0507
	6	III B	0.4107	0.1061	-0.0148	-0.3087	-0.0695	-0.1738	-0.2798	0.1440	-0.0421	0.0441
	6	III C	0.1854	-0.4024	-0.4801	0.1132	-0.0831	-0.1317	-0.0189	-0.0228	-0.0243	0.0661
	6	III D	0.1063	0.5145	-0.2019	-0.0723	0.0943	0.3288	-0.1223	-0.0364	-0.3005	0.3885
	6	III E	0.3396	0.2389	0.0792	0.1604	-0.1929	0.0204	-0.0097	-0.0939	0.0994	0.1306
	6	IV A	0.3714	0.0839	-0.0043	-0.1860	-0.2179	-0.0049	0.1310	-0.0465	0.1437	0.0240
	6	IV B	0.2471	0.0447	-0.0975	-0.2858	-0.2144	0.2756	0.2773	-0.1665	0.0792	-0.1635
	6	IV C	-0.1421	-0.4119	-0.7476	0.2183	0.0410	-0.0052	0.0322	0.0366	0.0335	0.0322
	6	IV D	-0.2228	0.5209	-0.2602	-0.0009	0.4031	-0.0898	-0.0601	-0.3444	0.0380	-0.3065
	6	IV E	0.3414	-0.1929	0.1315	-0.2607	0.0696	0.0411	0.1549	-0.0487	0.1914	-0.0808

PRINCIPAL CO-ORDINATE

NUMBER OF CO-ORDINATE			11	12	13	14	15	16	17	18	19
% VARIANCE			3.1286	2.9526	2.6599	2.4093	2.3167	2.0426	1.8085	1.5296	0.0000
	6	I A	0.1176	0.1761	0.0303	0.2196	0.0699	0.1781	-0.0304	0.2088	-0.0889
	6	I B	-0.3547	-0.0811	0.2335	0.1643	-0.1504	-0.0198	0.0632	-0.0784	0.0548
	6	I C	0.2142	-0.0406	-0.1941	-0.0901	0.1735	-0.0160	-0.0305	0.0031	0.0000
	6	I D	0.0636	0.1442	0.0018	-0.2688	-0.0453	-0.1887	0.0118	-0.1906	0.0688
	6	I E	0.0047	-0.2199	-0.1552	-0.0473	0.0003	-0.0044	0.0041	0.0641	-0.0261
	6	II A	-0.0488	0.1141	-0.0026	0.0589	-0.0430	-0.0315	0.0293	-0.0252	0.0147
	6	II B	0.0785	-0.1166	0.2212	-0.1329	0.1187	0.1901	0.2218	-0.0516	-0.0154
	6	II C	0.1762	-0.1865	-0.1280	0.1799	-0.2567	-0.0432	-0.2063	-0.1111	-0.0270
	6	II D	-0.0501	-0.0765	0.0119	0.0258	0.1410	-0.0440	-0.0393	-0.0325	0.0086
	6	II E	-0.1270	0.3865	0.0111	0.0056	-0.0245	-0.0104	-0.0991	0.0264	0.0270
	6	III A	0.1887	-0.1604	0.1685	-0.0111	-0.0964	-0.0154	0.0590	0.1378	0.2015
	6	III B	-0.1157	-0.0877	0.0664	0.0135	0.1870	0.0152	-0.0808	-0.1709	-0.2310
	6	III C	0.0185	0.0715	-0.1999	0.2118	0.0723	-0.1372	0.2695	-0.0556	0.0149
	6	III D	0.1189	0.0842	-0.0268	-0.0556	-0.0981	0.0624	0.0518	-0.0063	0.0141
	6	III E	-0.2268	-0.0813	-0.0308	-0.1129	0.0886	-0.2743	-0.0392	0.2636	-0.0103
	6	IV A	-0.1804	0.0327	-0.2158	-0.0270	0.0923	0.2549	-0.0852	-0.0690	0.2283
	6	IV B	0.2556	0.1231	0.2361	0.1081	0.0767	-0.1337	-0.0591	-0.0381	0.0019
	6	IV C	-0.0197	-0.0207	0.1367	-0.1788	-0.0391	0.1030	-0.2003	0.0512	-0.0327
	6	IV D	-0.0798	-0.1347	-0.0479	0.1019	0.0101	0.0290	0.0102	0.0113	-0.0083
	6	IV E	-0.0334	0.0736	-0.1162	-0.1648	-0.2768	0.0858	0.1495	0.0628	-0.1950

NUMBER OF CO-ORDINATE			PRINCIPAL CO-ORDINATE 1	2	3	4	5	6	7	8	9	10
% VARIANCE			22.4082	13.2779	11.4606	6.0526	5.7342	5.5484	5.1476	4.6765	3.6804	3.1802
SAMPLE	10	I A	-0.3341	0.0332	0.0028	0.5323	-0.0449	0.4396	0.2309	-0.2774	-0.0496	-0.1329
	10	I B	0.1101	-0.1742	-0.5534	-0.2284	0.1219	-0.1092	0.2543	-0.4004	0.2751	0.0587
	10	I C	-0.1202	-0.3224	-0.4214	0.0513	-0.0384	-0.0646	-0.0575	-0.0288	-0.1451	0.2354
	10	I D	-0.2149	-0.2253	-0.4537	0.0441	-0.0193	0.2176	-0.1104	0.2225	-0.0685	-0.0254
	10	I E	-0.3850	-0.1081	-0.1156	0.0831	-0.1093	0.1620	-0.1498	0.2887	0.0644	0.2855
	10	II A	-0.5239	0.2333	0.1501	-0.2318	-0.1375	-0.1437	0.1687	-0.1010	-0.4000	0.1027
	10	II B	-0.5416	0.1680	0.1684	-0.1834	-0.1803	-0.1312	0.0871	0.0339	-0.0419	-0.1572
	10	II C	0.0547	-0.3046	-0.3917	-0.2200	0.0435	-0.0544	-0.0243	0.1256	-0.1049	-0.2884
	10	II D	-0.5546	0.2534	0.1978	-0.1420	-0.1226	0.0154	0.1514	-0.0060	0.2061	-0.0032
	10	II E	-0.4938	0.1114	0.1679	-0.1018	0.1394	0.0254	-0.1855	0.1310	0.3463	-0.0456
	10	III A	-0.2776	0.0716	0.2450	0.0006	0.6492	0.0085	-0.3167	-0.2016	-0.1317	0.0282
	10	III B	0.5325	-0.1013	0.3294	-0.1185	0.0320	0.1636	0.1600	0.0578	-0.0329	0.1254
	10	III C	0.3123	0.6510	-0.2592	0.3246	0.2715	-0.3209	0.2916	0.3007	0.0002	0.0241
	10	III D	0.4860	-0.1953	0.3206	-0.1211	0.0915	0.1794	0.1836	0.0909	0.0447	0.0897
	10	III E	0.2811	-0.3278	0.1624	-0.0358	0.0743	0.0567	0.0692	0.1664	-0.0590	-0.3131
	10	IV A	0.5252	0.4730	-0.1321	-0.1124	-0.2039	0.1146	-0.2651	-0.1235	0.0264	-0.0280
	10	IV B	0.4325	-0.2267	0.2976	-0.0454	-0.0439	-0.0189	0.0729	-0.0168	-0.0014	0.1448
	10	IV C	0.2172	-0.3063	0.1338	0.2330	-0.1094	-0.3623	-0.2072	-0.1379	-0.0470	-0.0280
	10	IV D	-0.0291	-0.2623	0.2576	0.3080	-0.2337	-0.3075	-0.0992	-0.0404	0.1539	-0.0295
	10	IV E	0.5234	0.5595	-0.1064	-0.0367	-0.1801	0.1300	-0.2539	-0.0838	-0.0349	-0.0433

NUMBER OF CO-ORDINATE			PRINCIPAL CO-ORDINATE 11	12	13	14	15	16	17	18	19
% VARIANCE			2.6629	2.4062	2.2622	2.0736	1.9327	1.6706	1.5385	1.3533	0.0000
SAMPLE	10	I A	0.0449	0.0529	-0.0636	0.0350	-0.0552	0.0615	-0.0068	0.0040	0.0175
	10	I B	-0.2031	0.0171	0.0247	-0.0488	-0.0039	0.0104	0.0328	-0.0136	0.0078
	10	I C	0.2132	-0.2214	0.0690	0.3028	0.0249	-0.0016	-0.0022	0.0430	0.0246
	10	I D	0.0181	0.1688	0.3039	-0.1898	0.0635	-0.1531	0.0109	0.0194	-0.0378
	10	I E	-0.2685	-0.0523	-0.2310	-0.0886	0.0256	0.1411	0.0064	-0.0165	0.0122
	10	II A	-0.1089	0.0470	-0.0294	-0.0530	-0.2096	-0.1399	0.0051	0.0133	0.0389
	10	II B	-0.0813	0.1150	0.1369	0.1528	0.2047	0.2447	0.0398	0.0455	-0.0969
	10	II C	0.1829	0.0944	-0.2894	-0.0091	-0.0498	0.0421	-0.0637	-0.1171	-0.0604
	10	II D	0.2601	-0.2583	-0.0435	-0.1975	0.1536	-0.0962	-0.0315	-0.0274	0.0225
	10	II E	0.0841	0.1054	0.0746	0.1436	-0.2833	0.0056	0.0386	0.0123	0.0970
	10	III A	-0.0373	-0.0113	-0.0276	-0.0209	0.1302	-0.0231	-0.0351	-0.0187	-0.0461
	10	III B	0.0045	-0.0411	0.1859	-0.0059	-0.0732	0.1263	-0.1936	-0.2420	-0.0180
	10	III C	0.0134	0.0201	-0.0021	-0.0008	0.0026	0.0096	-0.0165	0.0192	0.0100
	10	III D	0.0622	-0.0144	-0.0623	0.0063	-0.0735	-0.0478	0.1148	0.1814	-0.2427
	10	III E	-0.2403	-0.2618	0.0362	0.0455	0.0249	-0.0644	0.0222	0.0780	0.1640
	10	IV A	-0.0131	0.0141	-0.0297	-0.0013	-0.0078	0.0074	-0.2552	0.2091	0.0048
	10	IV B	0.1213	0.3007	-0.0928	0.0197	0.1842	-0.0401	0.0582	0.0294	0.2234
	10	IV C	0.1042	-0.0649	0.0785	-0.2488	-0.1183	0.2002	0.0835	0.0548	0.0162
	10	IV D	-0.1306	0.0529	-0.0377	0.1081	0.0377	-0.2347	-0.1005	-0.0929	-0.1279
	10	IV E	-0.0257	-0.0629	-0.0008	0.0507	0.0227	-0.0481	0.2629	-0.1812	-0.0091

NUMBER OF CO-ORDINATE		PRINCIPAL CO-ORDINATE 1	2	3	4	5	6	7	8	9	10
% VARIANCE		24.4566	12.7103	9.1606	7.5172	6.0447	5.6749	4.6137	4.0336	3.8203	3.3476
8	I A	0.3316	0.3626	0.2850	-0.0861	0.1490	0.3126	0.0941	-0.3810	-0.0159	-0.4180
8	I B	0.3895	0.4171	0.2900	-0.0707	0.0362	0.2085	0.0991	0.0648	-0.0057	0.2604
8	I C	0.4079	0.4017	0.1614	-0.0133	0.0097	0.0587	0.1236	-0.0096	0.2221	0.3495
8	I D	0.1138	0.4163	0.2641	0.6026	-0.3620	-0.4818	-0.0843	-0.0324	-0.0321	-0.0999
8	I E	0.3690	0.3577	-0.2786	0.0716	0.5478	-0.1199	-0.1616	0.1786	-0.0799	0.0005
8	II A	0.4045	-0.0741	-0.3307	-0.1038	0.2615	-0.2339	-0.1981	-0.0291	-0.0491	-0.0679
8	II B	0.3576	-0.2162	-0.3731	-0.1648	-0.2618	-0.0951	0.0181	-0.1949	0.2453	0.0279
8	II C	0.3397	0.0820	0.0636	-0.3065	-0.3762	0.1705	-0.0005	0.4795	-0.2135	-0.1917
8	II D	0.4192	-0.0639	-0.3664	-0.2176	-0.2186	-0.0809	0.0028	0.0344	0.1854	-0.0744
8	II E	0.1681	-0.2307	-0.4708	0.4899	-0.0044	0.2173	0.2634	-0.0454	-0.2550	0.0304
8	III A	0.0576	-0.4846	0.4519	-0.0651	0.1317	-0.1334	-0.1154	0.0078	-0.1741	0.0225
8	III B	-0.1308	-0.4081	0.1048	0.1216	0.1532	-0.0991	0.5609	0.1283	0.0487	-0.0409
8	III C	-0.1361	-0.3273	0.0102	0.4387	-0.0605	0.4967	-0.3880	0.0705	0.1756	0.0276
8	III D	0.2486	-0.3913	0.1508	-0.1992	-0.1464	-0.0362	-0.0722	-0.2869	-0.1742	0.1449
8	III E	0.0393	-0.4646	0.3336	-0.0511	0.1472	-0.1234	-0.1085	0.0653	0.0667	0.0206
8	IV A	-0.6725	0.2093	-0.1091	-0.1057	-0.0663	-0.0088	-0.0568	-0.0384	-0.1848	0.0618
8	IV B	-0.7346	0.1491	-0.1254	-0.1052	-0.0105	0.0261	-0.0237	-0.0642	-0.0379	0.0226
8	IV C	-0.5772	-0.0041	0.0744	-0.0067	0.0993	-0.0547	0.0353	0.1183	0.3712	-0.1731
8	IV D	-0.6889	0.1597	-0.1190	-0.1353	-0.0574	-0.0197	-0.0082	-0.0948	-0.1464	0.0962
8	IV E	-0.7065	0.1095	-0.0166	-0.0932	0.0284	-0.0037	0.0199	0.0293	0.0537	0.0010

NUMBER OF CO-ORDINATE		PRINCIPAL CO-ORDINATE 11	12	13	14	15	16	17	18	19
		2.7619	2.5526	2.1867	1.9015	1.8481	1.7899	1.5096	1.0987	0.0000
8	I A	0.0671	0.0452	0.0287	-0.0197	-0.0011	-0.0045	-0.0344	-0.0064	0.0147
8	I B	-0.1111	-0.0493	-0.0467	0.0488	-0.1402	0.1793	0.2640	0.0842	-0.0060
8	I C	0.0079	0.0999	0.0316	-0.0257	0.0981	-0.0982	-0.2961	-0.0034	-0.0084
8	I D	0.0186	-0.0468	0.0154	-0.0216	-0.0070	0.0019	0.0258	0.0092	-0.0032
8	I E	0.1101	-0.0822	0.0053	0.0174	0.0655	-0.1226	0.1065	-0.1893	-0.0081
8	II A	-0.1397	-0.0871	-0.1053	-0.1158	-0.0877	0.1445	-0.1658	0.2344	0.0190
8	II B	-0.0066	0.0010	-0.0333	-0.0711	-0.2155	0.0713	0.0172	-0.2541	0.0212
8	II C	-0.0716	-0.0271	-0.0107	-0.1000	0.0062	-0.0356	-0.0785	-0.0549	0.0030
8	II D	0.2209	0.0737	0.1327	0.2493	0.1535	0.0001	0.1075	0.1635	-0.0276
8	II E	-0.2333	0.1928	0.0814	0.0576	0.0157	-0.0326	0.0034	0.0042	0.0133
8	III A	-0.0201	0.0399	0.0619	0.3224	-0.0357	0.1433	-0.1302	-0.1154	-0.0351
8	III B	0.2453	-0.1986	-0.1066	-0.0774	-0.0142	0.0313	-0.0173	0.0284	-0.0203
8	III C	0.1599	-0.1346	-0.0595	-0.0260	0.0056	0.0360	-0.0295	0.0210	0.0047
8	III D	-0.1192	-0.2264	-0.1339	-0.0357	0.1582	-0.2274	0.0954	0.0209	-0.0093
8	III E	0.0457	0.3372	0.1747	-0.2579	-0.0312	-0.0723	0.1246	0.0507	0.0283
8	IV A	0.2111	0.2516	-0.3424	0.0734	-0.1363	-0.0994	-0.0127	0.0414	-0.0125
8	IV B	-0.0411	-0.0872	0.2166	-0.0812	-0.0428	0.0074	-0.0134	0.0074	-0.3052
8	IV C	-0.3471	0.0716	-0.2066	0.0740	0.1391	-0.0056	0.0519	-0.0311	-0.0182
8	IV D	0.0705	0.0018	0.0597	-0.1212	0.2560	0.2571	0.0078	-0.0718	0.1457
8	IV E	-0.0676	-0.1755	0.2372	0.1106	-0.1861	-0.1740	-0.0263	0.0610	0.2041

			PRINCIPAL CO-ORDINATE								
NUMBER OF CO-ORDINATE		1	2	3	4	5	6	7	8	9	10
% VARIANCE		22.8307	17.6329	12.7663	7.3021	6.0757	5.7117	5.4819	3.6740	2.9786	2.7888
SAMPLE	3 I A	0.2323	-0.0278	0.0907	0.8188	-0.0781	-0.1203	-0.4889	0.0368	0.0291	0.0361
	3 I B	0.1716	-0.3661	0.0649	0.4487	0.4156	0.4047	0.5182	0.0042	-0.0116	-0.0346
	3 I C	0.2464	-0.6169	0.0042	-0.1057	-0.1525	0.0101	-0.0655	-0.6400	-0.0380	-0.0267
	3 I D	0.3492	-0.8148	-0.0614	-0.2010	-0.0396	-0.0743	-0.0477	0.2443	0.0107	0.0015
	3 I E	0.3512	-0.8089	-0.0603	-0.1979	-0.0473	-0.0916	-0.0736	0.2582	0.0204	0.0061
	3 II A	-0.3977	0.0398	0.0665	0.0395	-0.3911	0.2738	0.0208	0.0469	-0.1772	0.0420
	3 II B	-0.4450	0.0792	-0.5300	-0.0063	0.1280	-0.1255	-0.0019	-0.0366	0.2267	-0.0249
	3 II C	-0.4515	0.0461	-0.5513	0.0103	0.1344	-0.1459	0.0139	-0.0421	0.2743	-0.0281
	3 II D	-0.3605	0.0816	-0.5058	0.0096	0.1850	-0.1771	-0.0137	-0.0141	-0.4049	-0.0051
	3 II E	-0.4728	0.0780	-0.3362	-0.0297	-0.1573	0.1556	0.0038	0.0622	-0.1590	0.0311
	3 III A	0.5990	0.4049	-0.0675	0.0095	-0.1702	-0.2210	0.2685	-0.0034	0.0859	0.0637
	3 III B	0.5011	0.3496	-0.0116	0.0840	-0.3166	-0.3010	0.3651	0.0128	-0.0494	0.1672
	3 III C	0.4819	0.4015	-0.0302	-0.2266	0.2107	0.2858	-0.2505	0.0052	-0.1000	0.2029
	3 III D	0.5753	0.4067	-0.1026	-0.2174	0.2300	0.2404	-0.1925	-0.0250	0.1152	0.1187
	3 III E	0.4956	0.4161	0.0579	-0.0768	-0.0656	0.0505	-0.0431	0.0325	-0.0237	-0.5544
	3 IV A	-0.4435	0.0926	0.0590	-0.0443	-0.2602	0.2338	-0.0247	0.0823	0.0672	-0.0925
	3 IV B	-0.4434	0.0610	0.4365	-0.0822	-0.0189	0.0132	0.0106	0.0035	0.1035	0.0470
	3 IV C	-0.3932	0.0291	0.4034	-0.0567	-0.1247	0.1202	0.0238	-0.0144	0.1917	0.0754
	3 IV D	-0.2442	0.0791	0.5285	-0.0944	0.3535	-0.3433	-0.0172	-0.0072	-0.1096	-0.0505
	3 IV E	-0.3517	0.0693	0.5452	-0.0814	0.1649	-0.1881	-0.0054	-0.0062	-0.0515	0.0252

			PRINCIPAL CO-ORDINATE							
NUMBER OF CO-ORDINATE		11	12	13	14	15	16	17	18	19
% VARIANCE		2.0946	1.8179	1.7589	1.4699	1.1997	0.9537	0.7317	0.2596	0.0000
SAMPLE	3 I A	0.0155	0.0204	-0.0043	0.0065	0.0009	0.0132	0.0026	-0.0016	-0.0033
	3 I B	0.0150	-0.0103	0.0008	-0.0088	-0.0084	0.0028	0.0024	-0.0025	0.0039
	3 I C	0.0461	-0.0016	-0.0122	-0.0035	-0.0090	0.0048	0.0025	-0.0018	0.0021
	3 I D	-0.0154	-0.0013	0.0024	-0.0045	0.0018	-0.0008	0.0019	0.0031	-0.1412
	3 I E	-0.0129	0.0053	0.0061	-0.0001	-0.0025	0.0059	0.0009	-0.0033	0.1388
	3 II A	-0.2518	-0.1593	-0.1075	-0.1226	0.1316	-0.1527	0.0107	0.0371	0.0034
	3 II B	-0.0498	-0.0977	0.0403	-0.0628	-0.0037	-0.0416	0.2365	-0.1226	-0.0008
	3 II C	0.0011	-0.0989	0.0069	-0.0603	0.0500	-0.0104	-0.2238	0.1114	0.0005
	3 II D	-0.1872	0.1458	0.0611	0.1029	-0.1530	0.0053	-0.0006	0.0466	0.0003
	3 II E	0.2843	0.1246	-0.0510	0.0371	0.2213	0.1525	-0.0255	-0.0882	-0.0010
	3 III A	0.0087	0.3329	-0.1138	-0.1925	-0.0068	-0.0894	0.0062	0.0058	0.0000
	3 III B	0.0490	-0.2626	0.0939	0.1546	-0.0251	0.0731	0.0007	-0.0016	-0.0002
	3 III C	0.1298	-0.0746	0.2358	-0.2062	-0.0372	-0.0199	-0.0043	0.0201	0.0001
	3 III D	-0.1352	-0.0073	-0.2566	0.2398	0.0268	0.0145	-0.0024	-0.0127	-0.0005
	3 III E	-0.0602	-0.0310	0.0849	-0.0067	0.0429	0.0545	-0.0083	-0.0090	0.0003
	3 IV A	0.2692	-0.0130	-0.0931	0.0748	-0.2982	-0.1003	-0.0003	0.0198	-0.0005
	3 IV B	-0.0782	0.0432	-0.0359	-0.0792	-0.0313	0.2579	0.1183	0.1625	-0.0001
	3 IV C	-0.1363	0.1990	0.2880	0.1897	0.0566	-0.0747	-0.0424	-0.0451	-0.0016
	3 IV D	0.2037	-0.0437	-0.0489	0.0726	0.1467	-0.1681	0.0592	0.0741	0.0016
	3 IV E	-0.0956	-0.0698	-0.0971	-0.1308	-0.1034	0.0736	-0.1341	-0.1920	-0.0018

NUMBER OF CO-ORDINATE			PRINCIPAL CO-ORDINATE 1	2	3	4	5	6	7	8	9	10
% VARIANCE			15.4513	12.2137	9.7800	9.4171	7.0032	5.5220	4.9976	4.7354	4.1517	3.9160
SAMPLE	11	I A	-0.0029	0.5095	0.0090	0.5609	-0.0768	-0.0729	0.2064	-0.0998	0.1141	0.2239
	11	I B	-0.2094	0.3468	-0.0024	-0.0038	0.2827	0.2484	0.2217	0.1672	0.1248	-0.3661
	11	I C	-0.2778	0.3126	-0.1844	-0.5692	0.3011	-0.1871	0.2653	0.1986	-0.0503	0.2443
	11	I D	-0.3461	0.4488	-0.3092	-0.4438	-0.2460	0.1790	-0.3371	-0.2610	-0.0460	-0.0261
	11	I E	-0.1294	0.5505	0.0428	0.4144	-0.0528	-0.0096	-0.3176	0.1481	-0.0803	0.0547
	11	II A	0.1920	-0.0546	0.2370	0.0196	0.1080	0.3980	-0.0299	0.1366	0.0646	-0.0162
	11	II B	0.5070	0.0189	-0.3181	-0.0648	-0.1960	-0.1400	0.1648	-0.0445	-0.0447	-0.1170
	11	II C	0.3970	0.0239	-0.1335	0.1124	-0.2238	0.1357	0.3167	-0.0137	-0.4049	-0.0393
	11	II D	0.2456	-0.0840	0.3948	-0.0821	-0.0250	0.1729	0.1134	-0.3007	0.2164	0.1398
	11	II E	0.4120	-0.1584	-0.0076	-0.2738	-0.0807	0.2385	-0.0186	-0.0212	0.1172	0.0780
	11	III A	-0.1791	0.0985	0.4707	-0.0519	0.0775	-0.3058	0.0411	-0.3732	-0.0862	-0.1391
	11	III B	0.4814	0.0189	-0.1844	-0.0295	0.0516	-0.2457	-0.1711	0.0254	0.3989	-0.0693
	11	III C	0.2010	-0.0975	0.2196	0.0614	0.1821	0.0836	-0.2489	0.2630	-0.1515	0.0494
	11	III D	0.4320	-0.1342	-0.1802	0.0072	0.0626	-0.3114	-0.1703	0.0877	-0.1007	-0.1266
	11	III E	0.0145	-0.1787	0.3774	-0.1450	0.2132	-0.1385	-0.0822	0.0333	-0.1608	0.2142
	11	IV A	-0.4606	-0.2930	-0.0257	0.1634	-0.0450	-0.1637	0.1364	0.1332	0.1919	-0.0774
	11	IV B	-0.1726	-0.4088	-0.3548	0.2874	0.3045	0.0984	-0.0814	-0.2300	-0.1088	0.0835
	11	IV C	-0.3593	-0.3140	0.0178	-0.0309	-0.5669	-0.0147	0.0270	0.2287	0.0827	0.2012
	11	IV D	-0.3290	-0.1930	0.3178	-0.0714	-0.2440	-0.0622	-0.0309	0.0492	-0.0904	-0.3120
	11	IV E	-0.4163	-0.4124	-0.3864	0.1396	0.1737	0.0972	-0.0050	-0.1269	0.0140	0.0001

NUMBER OF CO-ORDINATE			PRINCIPAL CO-ORDINATE 11	12	13	14	15	16	17	18	19
% VARIANCE			3.3052	2.9854	2.8440	2.4054	2.2012	1.9760	1.9507	1.5289	-0.0000
SAMPLE	11	I A	-0.1683	0.0196	0.0338	-0.2092	0.1354	0.0191	-0.1632	-0.0027	-0.0047
	11	I B	-0.0078	-0.0070	-0.0965	-0.0973	0.0217	-0.2220	0.1000	0.0969	0.0155
	11	I C	-0.0591	-0.0588	-0.0731	0.0683	-0.0162	0.1582	0.0157	-0.0626	0.0301
	11	I D	0.0001	0.0816	0.1393	-0.1423	-0.0722	-0.0514	-0.0484	-0.0361	0.0077
	11	I E	0.0402	0.0328	-0.0656	0.3331	-0.0145	0.0476	0.1524	0.0422	-0.0425
	11	II A	0.1160	0.0430	-0.1215	0.0261	-0.1790	0.1132	-0.2517	-0.1461	-0.1382
	11	II B	0.0428	0.0389	-0.0089	0.2653	0.1114	-0.2156	-0.1183	-0.2009	0.0545
	11	II C	0.0878	-0.1140	0.1634	-0.0597	-0.1671	0.0965	0.0937	0.1171	-0.0301
	11	II D	-0.1693	0.1149	-0.0198	0.1231	-0.1679	-0.0016	0.1309	0.0121	0.1980
	11	II E	0.0368	0.1042	0.0049	-0.0043	0.3679	0.1106	0.1223	0.0908	-0.1438
	11	III A	0.3611	-0.0589	-0.1411	-0.0424	0.0681	0.0530	-0.0077	-0.0068	-0.0215
	11	III B	0.0345	-0.3492	0.1166	-0.0349	-0.1244	0.0379	0.0143	0.0600	-0.0460
	11	III C	0.1306	-0.0800	0.1493	-0.1439	0.1382	0.0034	-0.0114	-0.0882	0.2674
	11	III D	-0.1377	0.3431	-0.2322	-0.1694	-0.0948	0.0618	-0.0102	0.0909	0.0226
	11	III E	-0.1175	0.0167	0.1679	0.0349	-0.0407	-0.2919	-0.0650	0.1161	-0.1609
	11	IV A	0.1420	0.2939	0.3196	-0.0055	-0.0564	0.0584	0.0902	-0.1165	-0.0482
	11	IV B	-0.1093	-0.1365	-0.1209	-0.0812	-0.0016	-0.0412	0.1707	-0.2130	-0.0759
	11	IV C	0.1207	-0.1070	-0.2554	-0.0979	-0.0384	-0.1280	0.0367	0.0331	0.0246
	11	IV D	-0.4102	-0.1646	0.0324	0.0618	0.0863	0.1355	-0.0518	-0.0460	-0.0127
	11	IV E	0.0667	-0.0127	0.0079	0.1754	0.0442	0.0565	-0.1991	0.2597	0.1041

NUMBER OF CO-ORDINATE			PRINCIPAL CO-ORDINATE 1	2	3	4	5	6	7	8	9	10
% VARIANCE			22.0443	16.2192	10.8326	9.0334	7.6021	5.6140	5.2095	4.4091	3.0284	2.9422
SAMPLE	4	I A	0.1675	-0.7002	0.2398	-0.1715	0.1192	-0.5944	0.1479	-0.1639	0.0122	-0.2612
	4	I B	0.2964	0.0083	0.0291	0.7385	-0.1231	-0.0584	0.0805	-0.0041	0.0289	0.0299
	4	I C	0.2757	0.0533	-0.0090	0.7111	-0.0361	-0.0934	0.0821	0.1087	-0.0032	0.0043
	4	I D	0.2108	-0.7626	0.3162	-0.1374	0.1644	0.0512	0.0068	0.1092	-0.0056	0.4927
	4	I E	0.2674	-0.5913	0.2542	0.0140	0.0890	0.6037	-0.0924	0.1339	0.0131	-0.3272
	4	II A	0.3428	0.3448	-0.0464	-0.1564	0.1414	-0.1246	-0.1995	0.2838	-0.0455	0.0202
	4	II B	0.5389	0.3647	-0.0536	+0.2143	0.0308	-0.0895	-0.0055	0.2537	0.0008	-0.0323
	4	II C	0.5904	0.2489	-0.0019	-0.1301	-0.0750	0.1468	0.0281	-0.4255	-0.0070	0.0509
	4	II D	0.4898	0.3311	-0.0559	-0.2485	0.0250	-0.0740	0.0196	0.2174	0.0320	-0.0616
	4	II E	0.5949	0.2778	-0.0109	-0.1289	-0.0694	0.1180	0.0372	-0.3836	0.0016	0.0548
	4	III A	-0.3933	0.0260	-0.2317	0.1151	0.4606	0.0007	-0.2518	-0.1869	-0.0176	-0.0133
	4	III B	-0.3418	0.1048	-0.2129	0.0570	0.4369	-0.0331	-0.2651	-0.0453	0.0228	-0.0050
	4	III C	-0.5301	0.1202	0.1401	0.0515	0.1254	0.0107	-0.1062	-0.0766	-0.2080	0.0050
	4	III D	-0.1145	-0.4048	-0.6768	-0.0953	-0.4252	0.0072	0.0015	0.0407	-0.4175	-0.0018
	4	III E	-0.2196	-0.3027	-0.6795	-0.0788	-0.1817	0.0193	-0.0142	0.0227	0.4554	0.0324
	4	IV A	-0.4650	0.1879	0.0582	-0.1274	0.0279	0.0902	0.4328	0.0521	0.0157	-0.0120
	4	IV B	-0.4228	0.1041	0.3886	-0.0464	-0.4405	-0.0593	-0.2851	-0.0223	0.0763	-0.0041
	4	IV C	-0.4151	0.1449	0.3883	-0.0593	-0.4233	-0.0509	-0.2286	0.0029	0.0652	0.0017
	4	IV D	-0.5294	0.1554	0.0467	-0.0640	0.0622	0.1041	0.4194	-0.0172	0.0354	-0.0022
	4	IV E	-0.3431	0.2895	0.1174	-0.0289	0.0914	0.0254	0.1925	0.1001	-0.0550	0.0287

NUMBER OF CO-ORDINATE			PRINCIPAL CO-ORDINATE 11	12	13	14	15	16	17	18	19
% VARIANCE			2.2215	1.8189	1.6787	1.5751	0.8787	0.8496	0.7110	0.6483	0.0000
SAMPLE	4	I A	-0.0498	-0.0087	-0.0093	0.0115	-0.0034	-0.0021	-0.0010	0.0007	0.0022
	4	I B	-0.0320	-0.0527	-0.1971	-0.2715	0.0341	-0.0081	-0.0437	0.0199	0.0093
	4	I C	0.0573	0.0502	0.2119	0.2649	-0.0140	0.0123	0.0595	-0.0222	-0.0114
	4	I D	0.0529	0.0022	0.0047	0.0006	0.0023	-0.0005	-0.0005	0.0017	0.0001
	4	I E	-0.0344	-0.0087	-0.0044	0.0064	-0.0062	-0.0049	-0.0023	-0.0038	0.0015
	4	II A	-0.3750	-0.0787	0.0818	-0.1065	-0.0497	0.0290	0.1080	-0.0582	-0.0580
	4	II B	0.0702	0.0482	0.1494	-0.0348	0.0062	-0.0528	-0.2180	0.1051	0.0610
	4	II C	-0.0674	-0.0214	0.0166	0.0356	0.0250	0.1364	0.0622	0.1715	-0.0260
	4	II D	0.3576	0.1236	-0.2029	0.0062	0.0272	0.0443	0.1134	-0.0438	-0.0479
	4	II E	-0.0284	-0.0051	0.0029	0.0314	-0.0070	-0.1411	-0.0462	-0.1914	0.0307
	4	III A	0.1784	0.0374	0.0832	-0.1192	-0.2776	-0.0072	0.0329	0.0156	0.0402
	4	III B	0.0555	-0.2708	-0.0642	0.1030	0.2631	-0.0200	-0.0377	0.0058	-0.0213
	4	III C	-0.1259	0.4208	-0.0259	-0.0124	0.1618	0.0124	-0.0268	-0.0085	-0.0062
	4	III D	0.0395	-0.0814	-0.0051	0.0027	-0.0147	-0.0048	-0.0001	0.0000	-0.0054
	4	III E	-0.1180	0.1381	-0.0249	0.0287	0.0118	0.0050	-0.0049	0.0011	0.0120
	4	IV A	0.0371	-0.0764	0.1347	-0.1148	0.1207	0.0130	0.1167	-0.0138	0.1620
	4	IV B	0.0832	-0.0836	0.0526	-0.0120	-0.0246	0.1943	-0.0851	-0.0949	0.0241
	4	IV C	0.0312	-0.0317	-0.0016	0.0141	-0.0154	-0.2142	0.0963	0.1039	-0.0280
	4	IV D	0.0350	-0.0467	0.0707	-0.0481	-0.0527	-0.0049	-0.0754	-0.0133	-0.2185
	4	IV E	-0.1669	-0.0547	-0.2730	0.2144	-0.1870	0.0140	-0.0472	0.0245	0.0797

NUMBER OF CO-ORDINATE			PRINCIPAL CO-ORDINATE 1	2	3	4	5	6	7	8	9	10
% VARIANCE			21.4115	13.0314	10.8030	8.4308	7.3541	6.0733	4.3080	4.1546	3.8830	3.4479
SAMPLE	CLY	I A	0.3037	0.0347	-0.0498	-0.0347	-0.2054	0.1696	0.1976	-0.1177	0.1610	-0.0188
	CLY	I B	-0.1688	-0.0632	-0.1968	-0.0735	-0.0380	0.0916	0.1133	0.0470	0.0547	0.1021
	CLY	I C	-0.2070	0.0265	0.3417	-0.0959	-0.0356	-0.1402	0.0914	-0.0542	0.1633	-0.1493
	CLY	I D	-0.2681	-0.1598	0.0700	-0.0534	-0.0808	0.0504	-0.0097	0.2077	0.1188	-0.0134
	CLY	I E	-0.0567	-0.0076	-0.0448	-0.2458	-0.0753	0.0672	0.1062	0.2558	-0.1222	0.0412
	CLY	II A	0.3834	-0.2246	-0.0444	-0.1826	0.0147	0.0146	-0.2646	0.0443	0.0523	-0.0682
	CLY	II B	-0.1803	-0.1221	-0.3157	-0.0109	0.1540	0.0213	0.0424	-0.0279	0.0257	-0.0775
	CLY	II C	0.1676	-0.0094	0.0264	-0.1155	0.1750	0.0068	0.1284	-0.1765	-0.2196	-0.0242
	CLY	II D	-0.4021	-0.1508	0.1521	0.1807	0.0219	0.1895	-0.0697	-0.1040	0.0303	-0.1681
	CLY	II E	-0.0195	-0.0004	-0.0440	-0.2222	0.0042	-0.0363	0.1124	-0.0898	-0.0712	0.0187
	CLY	III A	-0.2489	-0.1629	0.2584	0.1594	-0.0095	0.2412	-0.0725	-0.0449	-0.1749	0.1665
	CLY	III B	0.3818	-0.1484	-0.0274	-0.1256	0.0304	0.0822	-0.1874	-0.0402	0.0427	0.0428
	CLY	III C	0.1160	0.5605	0.1178	-0.0875	0.2178	0.0846	-0.0701	0.0518	-0.0440	-0.1302
	CLY	III D	-0.1185	0.4877	-0.0411	0.1395	0.0290	0.0565	-0.0620	0.0787	0.0852	0.1363
	CLY	III E	0.0864	-0.1115	0.2727	0.0004	0.2507	-0.2381	0.0329	-0.0383	0.1361	0.2307
	CLY	IV A	0.5513	-0.1348	0.0396	0.4401	0.0578	-0.0392	0.1415	0.1754	-0.0472	-0.0889
	CLY	IV B	-0.1549	-0.0135	0.1191	-0.0248	-0.2236	-0.3022	-0.0631	0.0643	-0.1757	-0.0629
	CLY	IV C	0.2189	0.1876	-0.0168	0.1000	-0.3849	-0.0410	-0.0634	-0.1326	-0.0223	0.0667
	CLY	IV D	-0.2113	0.0593	-0.2903	0.1221	-0.0417	-0.1707	-0.0715	-0.0701	0.0075	-0.0087
	CLY	IV E	-0.1731	-0.0475	-0.3265	0.1303	0.1394	-0.1078	-0.0324	-0.0288	-0.0006	0.0053

NUMBER OF CO-ORDINATE			PRINCIPAL CO-ORDINATE 11	12	13	14	15	16	17	18	19
% VARIANCE			2.4999	2.1984	2.0507	1.8609	1.6495	1.5230	1.3262	1.0461	0.0000
SAMPLE	CLY	I A	0.1030	0.0945	0.0301	0.0270	0.0536	-0.1473	-0.0197	0.0233	0.0025
	CLY	I B	-0.0210	-0.0018	-0.0347	-0.0220	-0.0872	0.0323	0.1569	-0.0912	-0.1249
	CLY	I C	-0.0225	-0.1711	0.1311	0.0192	0.0164	0.0408	-0.0109	-0.0638	-0.0151
	CLY	I D	-0.0477	0.0964	0.0418	-0.1581	-0.1379	-0.0059	-0.0551	0.0608	0.0625
	CLY	I E	0.0245	-0.1463	-0.0913	-0.0005	0.1457	-0.0100	-0.0447	0.0289	0.0070
	CLY	II A	-0.0139	-0.0444	-0.0642	0.1100	-0.0927	-0.0750	-0.0673	-0.0691	-0.0288
	CLY	II B	0.0102	0.0922	-0.0063	0.0265	0.0747	0.0721	-0.0123	-0.1389	0.1270
	CLY	II C	-0.1985	-0.0137	0.0047	-0.1204	-0.0418	-0.0787	-0.0415	-0.0195	-0.0068
	CLY	II D	-0.0700	0.0280	-0.1719	0.0198	0.0673	0.0170	0.0142	0.0717	-0.0464
	CLY	II E	0.0140	0.0411	0.0095	0.1798	-0.1110	0.1245	-0.0083	0.1266	0.0229
	CLY	III A	0.1286	-0.0427	0.1063	0.0462	-0.0312	-0.0295	-0.0055	-0.0480	0.0335
	CLY	III B	-0.0620	0.0083	0.1356	-0.0718	0.1282	0.0773	0.1081	0.0744	0.0042
	CLY	III C	0.1765	0.0381	-0.0279	-0.0615	-0.0413	0.0109	0.0498	-0.0047	-0.0012
	CLY	III D	-0.2215	0.0287	0.0476	0.1083	0.0307	-0.0275	-0.0453	-0.0061	-0.0020
	CLY	III E	0.0579	0.0421	-0.1307	-0.0213	0.0357	-0.0143	-0.0001	0.0052	0.0147
	CLY	IV A	-0.0199	-0.0280	0.0115	0.0382	-0.0317	0.0408	0.0288	0.0097	0.0038
	CLY	IV B	-0.0002	0.1865	0.0356	0.0368	0.0590	-0.0562	0.0532	-0.0267	-0.0330
	CLY	IV C	0.0147	-0.0389	-0.1006	-0.0973	-0.0209	0.1271	-0.0654	-0.0454	0.0176
	CLY	IV D	0.0270	-0.1639	-0.0196	-0.0097	-0.0461	-0.1169	0.1069	0.0700	0.0827
	CLY	IV E	0.1210	-0.0051	0.0933	-0.0493	0.0307	0.0185	-0.1418	0.0429	-0.1204

APPENDIX 5

MEASURES OF NEMATODE DENSITY

Tables A5.1, A5.2 and A5.3 show the results of Principal Co-ordinate Analysis for species density data from the Hunter River sites expressed as number of animals per cm^2, number of animals per gram wet weight of the sediment and number of animals per sample respectively.

The units for density, as well as the omission of the two south coast estuaries have little effect on the main results of the analysis.

Principal Co-ordinate Analysis of data from the Hunter River expressed by the number of animals per cm²

•PERCENTAGE VARIANCE•

PCOROO 1										
5.5766	5.4463	4.9324	4.1[illegible]	3.6256	3.1985	3.0334	2.7306	2.4084	2.3083	2.2134
2.1145	1.9[illegible]	1.8[illegible]	1.[illegible]	1.4525	1.3624	1.3136	1.2486	1.2309		

••• LATENT VECTORS(COORDINATES) •••

	PCOCOO 1	2	3	4	5	6	7	8	9	10
1	-0.2619	0.2756	-0.1316	-0.0272	0.1767	0.0377	-0.1152	0.0301	0.0294	0.1703
2	-0.1668	0.1579	-0.1116	-0.1927	0.1515	-0.0898	-0.0801	0.0589	-0.0635	0.1335
3	0.0319	0.0739	-0.1201	-0.1485	0.1393	-0.0363	-0.1127	0.3017	0.0571	0.1558
4	-0.1355	0.0379	-0.1355	-0.0592	0.1372	-0.0893	0.3415	-0.0027	-0.0182	0.1627
5	-0.1756	0.0012	-0.1053	-0.2266	0.1553	-0.0140	-0.0299	0.1081	-0.0992	0.0593
6	0.1456	-0.1638	-0.2514	-0.1117	0.1649	0.1154	-0.1846	-0.0846	-0.0956	0.0930
7	0.0636	-0.0038	-0.1214	-0.1207	0.1402	-0.0278	-0.0655	0.1044	0.0150	0.0290
8	0.0761	-0.0441	-0.2321	-0.0405	0.0590	0.0174	-0.0[illegible]	0.0912	0.0308	0.2438
9	0.3722	-0.1118	-0.0941	-0.1039	-0.1078	-0.0501	-0.[illegible]	0.0244	0.0959	0.1716
10	0.3831	-0.0367	-0.1747	-0.1073	-0.0792	-0.0913	0.0700	0.0911	0.0203	-0.0199
11	0.3651	-0.1414	-0.[illegible]	-0.1165	-0.2261	0.1294	0.1[illegible]	0.1493	0.0[illegible]	0.1013
12	0.3554	-0.0543	-0.[illegible]	-0.[illegible]	-0.1932	0.1452	0.1[illegible]	0.0772	0.0[illegible]	0.1451
13	0.1662	-0.1905	-0.2652	-0.1696	-0.2064	0.1179	-0.1646	0.1720	-0.0306	0.2085
14	0.2196	-0.0245	-0.[illegible]	-0.[illegible]	-0.0066	0.0526	-0.1597	-0.0026	-0.0282	0.2836
15	0.3566	-0.0059	-0.[illegible]	-0.[illegible]	-0.0036	0.1223	-0.0365	-0.0249	-0.0320	0.1903
16	0.3907	-0.0554	-0.[illegible]	-0.[illegible]	-0.0461	0.1495	0.0363	0.0318	0.0220	0.2032
17	0.3326	-0.0591	-0.[illegible]	-0.[illegible]	-0.1207	0.1836	-0.0188	0.0255	-0.0569	0.0605
18	0.0741	-0.1769	-0.0668	-0.1547	-0.1445	0.1123	-0.2354	0.2146	-0.1723	0.0938
19	0.0241	-0.1569	-0.1471	-0.1160	-0.0691	0.1304	-0.1293	-0.0980	-0.0254	0.2983
20	0.4031	-0.1196	-0.3772	-0.1012	-0.0031	0.0979	-0.1121	0.3694	-0.1105	0.1761
21	0.3326	-0.0679	-0.[illegible]	-0.0830	-0.1654	-0.0479	-0.1731	-0.1232	-0.0274	0.1221
22	0.2671	-0.1322	-0.[illegible]	-0.[illegible]	-0.1469	-0.1972	0.0865	-0.0606	0.0655	0.1998
23	0.4686	-0.1161	-0.[illegible]	-0.[illegible]	-0.0270	-0.1749	0.0885	-0.0135	0.0606	0.2460
24	0.4161	-0.1198	-0.[illegible]	-0.[illegible]	-0.1065	-0.1087	0.0345	-0.0300	0.0820	0.1935
25	0.4601	-0.1527	-0.[illegible]	-0.[illegible]	-0.2184	-0.0891	-0.1460	-0.0895	0.0383	0.1730
26	0.4761	-0.1559	-0.[illegible]	-0.[illegible]	-0.2393	-0.0420	-0.2167	-0.0171	0.0499	0.0697
27	0.1919	-0.1568	-0.[illegible]	-0.[illegible]	-0.3965	-0.0067	-0.2405	-0.0365	0.0875	0.0092
28	0.3772	-0.1624	-0.[illegible]	-0.[illegible]	-0.0855	-0.2157	-0.1240	-0.0106	0.0749	0.0926
29	0.1624	-0.1641	-0.[illegible]	-0.[illegible]	-0.2552	-0.0355	-0.2251	-0.0918	0.0139	0.1240
30	0.2841	-0.1675	-0.[illegible]	-0.[illegible]	-0.2789	-0.0621	-0.2673	-0.0679	0.0701	0.0926
31	0.0437	-0.1666	-0.[illegible]	-0.[illegible]	-0.1141	-0.1708	-0.1954	-0.1320	0.0701	0.1240
32	0.2867	-0.1644	-0.[illegible]	-0.[illegible]	-0.1098	-0.1562	-0.1937	-0.1205	0.0701	0.1240
33	0.4212	-0.1676	-0.[illegible]	-0.[illegible]	-0.2231	-0.1426	-0.0344	-0.0265	0.0701	0.1240
34	0.1763	-0.1675	-0.[illegible]	-0.[illegible]	-0.0344	-0.1426	-0.0344	-0.0265	0.0701	0.1240
35	0.3705	-0.1675	-0.[illegible]	-0.[illegible]	-0.0344	-0.1426	-0.0344	-0.0265	0.0701	0.1240
36	0.4317	-0.1675	-0.[illegible]	-0.[illegible]	-0.0344	-0.1426	-0.0344	-0.0265	0.0701	0.1240
37	0.4317	-0.1675	-0.[illegible]	-0.[illegible]	-0.0344	-0.1426	-0.0344	-0.0265	0.0701	0.1240
38	0.4029	-0.0213	-0.[illegible]	-0.[illegible]	-0.1296	-0.2319	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
39	0.1496	-0.0551	-0.[illegible]	-0.[illegible]	-0.0571	-0.0792	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
40	0.1557	-0.0641	-0.[illegible]	-0.[illegible]	-0.0369	-0.0167	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
41	0.1687	-0.0576	-0.[illegible]	-0.[illegible]	-0.0818	-0.0818	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
42	0.2164	-0.0945	-0.[illegible]	-0.[illegible]	-0.0894	-0.0894	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
43	0.1344	-0.1009	-0.[illegible]	-0.[illegible]	-0.0485	-0.0485	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
44	0.3822	-0.0313	-0.[illegible]	-0.[illegible]	-0.0471	-0.0471	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
45	0.3666	-0.0402	-0.[illegible]	-0.[illegible]	-0.0417	-0.0417	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
46	0.2771	-0.0360	-0.[illegible]	-0.[illegible]	-0.0196	-0.0196	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
47	0.1612	-0.0442	-0.[illegible]	-0.[illegible]	-0.0111	-0.0111	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
48	0.2726	-0.0184	-0.[illegible]	-0.[illegible]	-0.0553	-0.0553	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
49	0.2577	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
50	0.2577	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
51	0.1761	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
52	0.2445	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
53	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
54	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
55	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
56	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
57	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
58	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
59	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
60	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
61	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
62	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
63	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
64	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
65	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
66	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
67	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
68	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
69	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
70	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
71	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
72	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
73	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
74	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
75	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
76	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
77	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
78	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
79	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
80	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
81	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
82	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
83	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
84	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
85	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
86	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
87	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
88	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
89	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
90	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
91	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
92	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
93	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
94	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
95	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
96	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
97	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
98	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
99	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
100	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
101	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
102	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
103	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
104	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
105	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
106	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
107	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
108	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
109	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
110	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
111	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
112	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
113	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
114	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
115	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
116	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
117	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
118	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
119	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
120	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
121	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
122	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
123	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
124	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
125	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
126	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
127	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
128	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
129	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
130	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
131	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
132	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
133	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
134	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
135	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
136	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
137	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
138	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
139	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]
140	0.2719	-0.0211	-0.[illegible]	-0.[illegible]	-0.0478	-0.0478	-0.[illegible]	-0.[illegible]	-0.[illegible]	-0.[illegible]

Principal Co-ordinate Analysis of data from the HUnter River expressed by the number of animals per gram wet weight of sediment

** PERCENTAGE VARIANCE **

1	2	3	4	5	6	7	8	9	10	11
2.8511	2.6365	2.7667	1.0455	2.7796	2.7612	3.0049	2.7801	2.4527	2.4128	2.1796

12	13	14	15	16	17	18	19	20
2.1252	1.8183	1.6260	1.5631	1.5054	1.4370	1.3304	1.2240	1.2061

** LATENT VECTORS(COORDINATES) ***

PCO	1	2	3	4	5	6	7	8	9	10
1	-0.1136	0.3928	-0.1358	0.0276	0.0960	-0.0050	-0.0005	-0.1351	0.0161	-0.0344
2	-0.1373	0.2783	-0.1655	0.1252	0.1293	-0.0119	-0.0503	-0.0117	0.0803	0.0169
3	-0.0552	0.4116	-0.1872	0.1027	0.1271	-0.0256	-0.0557	-0.0856	0.0416	0.0151
4	-0.1816	0.4017	-0.0991	0.0354	0.0038	0.0111	0.0281	-0.1663	-0.0468	-0.0601
5	-0.2498	0.3373	-0.1108	0.1481	0.1167	-0.0444	-0.0532	0.0815	0.0444	0.0925
6	0.2864	0.1117	-0.2410	-0.1395	0.1196	-0.0317	-0.0686	-0.1908	0.0373	-0.0668
7	0.3977	-0.0552	-0.1276	0.0371	0.0808	-0.0737	-0.0585	0.0651	-0.0517	-0.0282
8	0.4311	-0.0807	-0.2141	0.0258	0.0502	0.0162	-0.0577	0.0027	-0.1483	-0.0955
9	0.3795	-0.1252	-0.0324	0.1619	-0.1352	0.0223	0.0864	0.0387	-0.1255	0.0173
10	0.3966	-0.1373	-0.1095	0.1749	-0.1265	-0.0455	0.0151	0.1002	-0.0382	-0.0082
11	0.3578	-0.1856	-0.3069	0.1770	-0.1781	0.0287	0.0702	0.1014	-0.1431	-0.1162
12	0.3738	-0.1171	-0.4556	0.1358	-0.1789	0.1906	0.0650	0.0069	-0.1600	-0.0796
13	0.1749	-0.2417	-0.5558	0.1466	-0.1168	0.2464	-0.2371	-0.0642	-0.1008	-0.1767
14	0.2463	-0.0017	-0.2574	-0.0468	-0.0104	0.0008	-0.1087	-0.2042	-0.2159	-0.1379
15	0.3906	-0.0625	-0.5824	0.0029	-0.0564	0.0594	0.0178	-0.1092	-0.0742	-0.0851
16	0.4157	-0.1066	-0.3862	0.0571	-0.0488	0.1307	0.0469	-0.0361	-0.0937	-0.0526
17	0.2730	-0.1495	-0.4004	0.0027	0.1344	0.0671	0.0115	-0.0278	0.0464	-0.0471
18	-0.0698	-0.2091	-0.0368	0.1031	-0.0441	0.2295	-0.3424	-0.0770	0.0259	-0.1767
19	0.0567	-0.1237	-0.1900	-0.1122	0.0322	0.0208	-0.0200	-0.2471	-0.0863	-0.0681
20	0.4146	-0.1697	-0.3398	0.1167	-0.0600	0.1354	0.0728	0.0570	-0.1299	0.0095
21	0.1217	0.1431	-0.1417	-0.1872	0.1000	-0.0736	-0.0394	-0.2284	-0.0011	-0.0448
22	0.3647	-0.1077	-0.0626	0.0296	-0.0468	-0.1046	-0.0375	-0.0256	-0.1539	-0.0039
23	0.4231	-0.0223	-0.2217	-0.1975	0.1370	-0.0665	-0.0772	-0.0762	-0.1031	-0.0282
24	0.3677	-0.0869	-0.2214	-0.3323	0.1995	-0.1469	-0.0991	-0.1183	-0.0278	-0.0042
25	0.3013	0.0809	-0.1787	-0.1909	0.2499	-0.1114	-0.1768	-0.2303	-0.0322	-0.0345
26	0.2736	0.1826	-0.1611	-0.2141	0.2466	-0.1678	-0.1836	-0.0337	-0.0953	-0.0094
27	0.3491	0.1738	-0.1112	-0.1448	0.1610	-0.1111	-0.0497	-0.0974	-0.0741	0.0566
28	0.4564	-0.1496	-0.0225	-0.3215	0.2286	-0.1595	-0.1304	-0.1421	0.0276	-0.0005
29	0.2567	0.1906	-0.2025	-0.2701	0.1698	-0.2223	-0.1562	-0.0886	-0.0103	-0.0005
30	0.3246	0.0956	-0.1705	-0.1310	-0.0107	-0.2558	-0.1260	-0.0673	-0.0223	-0.0023
31	0.1777	0.1224	-0.1681	-0.2761	0.1887	-0.0459	-0.0414	-0.1591	0.1544	-0.0093
32	0.2817	-0.1670	0.3683	-0.1097	-0.1887	-0.0343	-0.1372	-0.1146	0.0246	-0.0110
33	0.0459	-0.0520	0.1947	-0.1674	-0.2634	-0.4979	-0.0415	-0.1134	0.2231	-0.0099
34	0.2736	-0.0931	0.3146	-0.1273	-0.1651	-0.4299	-0.0611	-0.0184	0.0487	-0.0099
35	0.3788	-0.1034	0.3147	-0.1835	-0.2628	-0.2719	-0.0455	-0.1202	0.1159	-0.0001
36	0.3171	-0.0967	0.2525	-0.2217	-0.2780	-0.4904	-0.0534	-0.0496	0.1026	-0.0175
37	0.4106	-0.1047	0.1606	-0.2050	-0.2342	-0.3333	-0.0229	-0.0146	-0.0310	-0.0320
38	0.2481	-0.1167	0.3745	-0.2021	-0.2994	-0.3772	-0.0425	-0.0221	-0.0267	-0.0502
39	-0.1459	0.3282	0.0162	-0.2089	-0.1577	-0.0191	0.1714	-0.2610	-0.1380	-0.0554
40	-0.1712	0.2511	0.0020	-0.2965	-0.1919	-0.0051	0.1786	-0.2419	-0.2005	-0.0724
41	-0.2002	0.1709	-0.0025	-0.2941	-0.2058	-0.0317	0.1772	-0.1674	-0.1588	-0.0619
42	-0.1200	0.1749	0.1004	-0.0475	-0.1539	-0.0755	0.0434	-0.0509	-0.1105	-0.0236
43	-0.3024	-0.0980	0.0396	-0.4229	-0.2679	-0.0774	0.2168	0.0144	-0.1814	-0.0055
44	-0.3165	-0.0983	-0.1464	-0.3185	-0.0733	-0.1826	0.0186	0.1561	0.0577	0.0415
45	-0.2588	0.0191	-0.1787	-0.2370	-0.0523	-0.1629	0.0475	0.0285	0.1260	-0.0290
46	-0.1260	0.1265	-0.1493	-0.3145	-0.0621	-0.1490	0.0780	-0.1437	-0.0454	-0.0509
47	-0.2460	-0.1421	-0.1411	-0.3974	-0.1464	-0.1667	0.1124	0.0422	0.0733	-0.0176
48	-0.2471	-0.2956	-0.0902	-0.2712	-0.0332	-0.0104	-0.1849	0.0369	0.0857	-0.0166
49	0.1478	0.0564	-0.2538	-0.2005	-0.0216	0.0238	0.1071	-0.0755	0.3807	0.0099
50	0.1566	-0.0893	-0.2571	-0.0348	-0.0899	0.0349	0.0940	0.0939	0.2027	0.0606
51	0.0634	-0.1989	-0.2270	0.0659	-0.0064	0.1034	-0.1718	0.0999	0.1117	-0.1166
52	0.0188	-0.1149	-0.2414	-0.2197	-0.0286	-0.1232	-0.0017	-0.0334	0.2085	-0.0332
53	0.0651	-0.0869	-0.2516	-0.1192	-0.0869	0.0880	0.1946	0.0072	0.2053	0.0857
54	0.2506	-0.1065	-0.1167	-0.2894	-0.3094	0.1598	0.1622	0.2441	-0.1771	0.0837
55	0.2758	-0.1257	-0.1925	-0.1148	-0.2804	0.1822	0.1731	0.2936	-0.1888	0.1414
56	0.2976	-0.0711	-0.3161	-0.3683	-0.3475	0.1658	0.1462	0.2223	-0.0998	0.0809
57	0.2708	-0.0580	-0.1065	-0.2971	-0.3349	0.1781	0.1610	0.2436	-0.2052	0.0963
58	0.3505	-0.1360	-0.1611	-0.2472	-0.2757	0.1758	0.1990	0.2826	-0.1778	0.1083
59	-0.1562	0.1262	0.0200	-0.0547	-0.0925	0.0203	0.0627	-0.2562	-0.1930	-0.0925
60	-0.1922	0.1886	0.0928	0.0361	-0.1329	0.0753	0.0437	-0.1585	-0.2105	-0.0643
61	-0.1200	0.1914	0.1094	-0.0610	-0.1540	0.0869	0.0381	-0.1208	-0.1519	-0.0379
62	-0.0824	0.1692	0.0877	-0.0515	-0.1240	0.0804	0.0450	-0.1875	-0.1596	-0.0443
63	-0.1575	0.3437	0.0539	-0.0222	-0.1171	0.0395	0.0404	-0.2133	-0.2409	-0.0814
64	-0.2206	0.3447	0.0620	0.1110	-0.0411	0.0066	-0.1472	-0.2598	-0.0874	-0.0304
65	-0.1758	0.3087	0.0219	0.0339	0.1135	-0.0787	-0.2250	-0.1800	0.0266	0.0781
66	-0.1470	0.3087	-0.0210	0.1001	0.0336	-0.0370	-0.1947	-0.2442	-0.0077	0.0000
67	-0.1420	0.3221	0.1135	0.0816	-0.0507	0.0340	-0.1699	-0.2084	-0.1221	-0.0138
68	-0.1537	-0.1018	0.0748	0.0831	-0.0087	0.0084	-0.2187	-0.3469	-0.0251	-0.0550
69	-0.1907	-0.0538	0.0610	0.0539	-0.0536	0.0651	-0.2510	-0.3181	-0.0876	-0.0852
70	-0.0134	0.3453	0.0811	0.0939	-0.1053	-0.0519	-0.2475	-0.3503	-0.0027	0.0392
71	-0.2059	0.3563	0.0393	0.1347	-0.0502	0.0257	-0.1475	-0.3360	-0.0291	0.0183
72	-0.1285	0.3719	0.0614	0.1285	-0.0345	-0.0079	-0.1687	-0.3565	-0.0532	-0.1068
73	-0.2520	0.3515	0.0645	0.0859	-0.1039	0.0525	-0.0894	-0.1722	-0.0720	-0.0311
74	-0.2582	0.4153	0.0371	0.0958	-0.1201	0.0345	-0.0918	-0.1320	0.1382	-0.0396
75	-0.2483	0.2858	0.0264	0.2411	-0.0199	-0.0325	0.0031	0.1475	0.3224	-0.0136
76	-0.2033	0.3413	0.0709	0.0702	-0.1198	0.0564	0.0749	0.0125	0.0855	0.0151
77	-0.2316	0.2426	0.0851	0.0875	-0.1369	0.0608	0.0447	-0.0051	-0.0755	-0.0008
78	-0.2127	0.3103	0.0556	0.1296	-0.0789	-0.0116	0.0425	0.0910	-0.2856	-0.0327
79	0.3063	-0.0074	0.1098	-0.1770	0.3367	-0.0253	-0.0797	0.1273	0.0157	0.0242
80	0.3299	-0.1041	0.3273	-0.1261	0.3671	0.1544	0.0657	0.1564	-0.0170	0.0401
81	0.3651	-0.0951	0.2296	-0.2107	0.3691	0.1239	0.0580	0.1506	-0.0130	0.1260
82	0.3105	0.0117	0.1619	-0.1850	0.3856	0.0652	0.0148	0.2051	0.0572	0.1370
83	0.3317	0.0151	0.2463	-0.2215	0.3840	0.1103	0.0222	0.2271	0.0158	0.1407
84	0.1573	0.0037	0.2940	-0.1362	0.2253	0.2449	0.1051	0.0642	0.0390	0.0192
85	0.2507	-0.0266	0.4280	-0.0264	0.0700	-0.1320	0.0266	0.0951	0.0604	0.0713
86	0.2459	-0.0783	0.4774	-0.0815	0.1686	0.2404	0.2093	-0.0065	0.0204	-0.0738
87	0.2569	-0.0522	0.4280	-0.1465	0.2775	0.2758	0.1815	0.1152	0.0143	0.0071
88	0.1826	-0.0702	0.4998	-0.0878	0.1778	0.3469	0.2490	-0.0011	0.0172	-0.0955
89	0.0819	-0.0715	0.5194	-0.0500	0.0869	0.1946	0.0645	-0.0473	-0.0691	-0.0417
90	0.1324	-0.0715	0.5126	-0.0419	0.0864	0.3406	0.2687	-0.0834	0.0449	-0.1676
91	0.0327	-0.0475	0.3216	-0.0733	0.1978	0.1507	-0.1527	0.0146	-0.1378	
92	0.0866	-0.0696	0.4886	-0.0172	-0.0091	0.2810	0.2441	-0.1507	0.0618	-0.1935
93	0.1274	-0.1014	0.4929	-0.0456	-0.0315	0.2675	0.2399	-0.1412	0.0413	-0.2106
94	0.2865	-0.0290	0.5541	-0.0936	0.1993	-0.0687	-0.1154	0.1331	-0.0121	-0.0562
95	0.3334	-0.0621	0.2720	-0.1290	0.2434	-0.0273	0.0086	0.1452	-0.0318	0.0440
96	0.2905	-0.1419	0.3728	-0.1058	-0.0898	-0.1238	0.0707	-0.0455	-0.0571	-0.0431
97	0.3660	-0.0119	0.1900	-0.1959	0.3270	0.0725	-0.0282	0.1355	-0.0920	0.0404
98	0.2942	0.0156	0.1872	-0.0964	0.1155	-0.1554	-0.0805	0.1116	0.0272	0.0893
99	0.1705	-0.1177	0.3077	-0.1546	-0.1744	-0.2613	-0.0360	-0.1580	0.0834	0.0552
100	-0.2172	-0.2266	-0.0056	-0.0682	-0.0024	0.0376	-0.2285	-0.0070	0.0257	0.0212
101	-0.2301	-0.2201	0.0841	-0.0403	-0.0727	0.1937	-0.3372	-0.1508	0.0355	0.4172
102	-0.1640	-0.2029	0.1368	-0.0076	-0.1320	0.3116	-0.4741	-0.2889	0.0496	0.4819
103	-0.1464	-0.1935	0.1354	-0.0051	-0.1543	0.3098	-0.4645	-0.5209	0.0354	0.4958
104	-0.3854	-0.2765	-0.0529	-0.1888	-0.0534	-0.0901	0.0384	0.1618	-0.0093	0.3184
105	-0.4555	-0.1661	0.0222	-0.4165	-0.2452	-0.1192	0.1093	0.1891	-0.1552	0.0829
106	-0.3935	-0.2227	0.0470	-0.4471	-0.2817	-0.1063	0.1923	0.1730	-0.1687	0.0588
107	-0.3238	-0.1222	0.0106	-0.3366	-0.1944	-0.1154	0.2219	0.1497	-0.1095	0.0929
108	-0.4564	-0.2573	-0.0104	-0.3272	-0.1548	-0.1182	0.1491	0.2051	-0.0804	0.1734
109	-0.1015	-0.1048	0.3044	-0.0337	-0.0455	0.2187	0.2334	-0.0216	0.4645	0.0722
110	0.0864	-0.0180	-0.2714	0.1012	-0.0578	0.2245	0.2656	0.0146	0.4151	0.1180
111	-0.0970	0.1482	-0.1705	0.0107	0.0043	0.1223	0.2448	-0.1709	0.4248	0.0881
112	-0.0031	0.1605	-0.2072	-0.0549	-0.0739	0.1689	0.2425	-0.1913	0.4348	0.0415
113	-0.0196	0.0720	-0.2466	-0.0638	-0.0946	0.1803	0.2139	-0.0525	0.4561	0.1387
114	-0.4705	-0.1480	0.0719	-0.1804	-0.0003	-0.1045	0.1413	0.1315	-0.0552	0.2790
115	-0.5022	-0.1855	-0.0528	0.0413	0.1897	-0.1390	0.1580	0.0046	-0.1248	0.2956
116	-0.4226	-0.3704	-0.0261	-0.0127	0.1060	-0.0796	0.0908	0.0283	-0.0788	0.3152
117	-0.4218	-0.2169	-0.0243	0.2221	0.2922	-0.1478	0.2452	-0.1280	-0.1567	0.1641
118	-0.4736	-0.3434	-0.0633	0.1619	0.2630	-0.1437	0.2188	-0.0908	-0.1288	0.2407
119	-0.0672	-0.0611	0.1332	0.0201	-0.1216	0.2124	-0.2169	-0.2056	-0.0053	0.1269
120	-0.2976	-0.1279	0.0558	0.0971	-0.0422	-0.0351	-0.0613	0.1245	0.2988	-0.2582
121	-0.3503	-0.0914	0.0254	0.0192	-0.0785	-0.0952	-0.0117	0.1618	0.2769	-0.2289
122	-0.1142	-0.1601	0.1529	0.0464	-0.1606	0.3164	-0.4473	-0.2762	0.0168	0.2668
123	-0.1810	-0.2796	0.1555	-0.0042	-0.1769	0.3386	-0.5396	-0.2070	0.0739	0.1445
124	-0.4608	-0.4440	-0.0471	-0.1019	-0.0148	-0.0063	-0.1126	-0.1680	0.0669	-0.1980
125	-0.3954	-0.4081	0.0159	-0.2161	-0.1246	0.0212	-0.1918	-0.2175	0.0047	-0.4497
126	-0.3015	-0.3605	0.0214	-0.1367	-0.1263	0.1300	-0.3397	0.1271	0.0574	-0.4484
127	-0.3947	-0.3019	0.0260	-0.0909	-0.0692	0.0736	-0.2375	0.1399	0.0529	-0.5546
128	-0.3361	-0.0095	0.0273	-0.1181	-0.1130	-0.1166	-0.3364	0.1894	0.0652	-0.4324
129	-0.3681	-0.1133	-0.0851	0.3339	0.3096	-0.1136	0.0121	0.0309	0.0245	-0.0275
130	-0.3965	-0.1683	-0.0654	0.4228	0.3794	-0.1119	0.0361	-0.0819	-0.1010	0.0095
131	-0.2071	-0.2142	0.0679	0.0601	-0.0542	-0.0282	-0.1286	-0.1964	-0.1748	-0.0217
132	-0.5033	-0.1270	0.0122	0.0970	-0.0824	-0.0372	0.1771	-0.1052	-0.1203	-0.0475
133	-0.3797	-0.1778	-0.0574	0.3838	0.3820	-0.0997	0.0998	-0.1605	0.0954	-0.1854
134	-0.2571	-0.1633	-0.0378	0.3427	0.3509	-0.0539	0.0154	-0.1794	-0.0678	-0.1317
135	-0.2809	-0.1954	-0.0332	0.3562	0.3170	-0.0351	0.0246	-0.1658	-0.0693	-0.1452
136	-0.3764	-0.1685	-0.0555	0.3959	0.4036	-0.1330	0.1207	-0.1476	-0.0735	-0.1219
137	-0.4398	-0.2145	-0.1050	0.3737	0.3933	-0.1068	0.0223	-0.0826	-0.0408	-0.1401

Principal Co-ordinate Analysis of data from the Hunter River expressed by the number of animals per sample

PERCENTAGE VARIANCE

PCOROO 1	2	3	4	5	6	7	8	9	10	11
8.7004	5.6896	4.9057	4.0605	3.6271	3.2839	3.0126	2.6973	2.4128	2.4070	2.1811
12	13	14	15	16	17	18	19	20		
2.0680	1.9520	1.7180	1.5220	1.3850	1.3576	1.3030	1.2503	1.1977		

*** LATENT VECTORS(COORDINATES) ***

PCOCOO	1	2	3	4	5	6	7	8	9	10
1	-0.0329	0.3155	-0.0847	-0.1210	0.1331	-0.0477	-0.0916	-0.0584	0.0887	-0.1058
2	-0.0940	0.2186	-0.1136	-0.2244	0.1206	-0.0102	-0.0978	0.0156	0.1257	-0.0019
3	0.0040	0.0796	-0.1016	-0.1774	0.0585	-0.0419	-0.1023	-0.0390	0.1750	-0.0750
4	-0.0404	0.1951	-0.1644	-0.1550	0.1219	-0.0653	-0.1378	-0.0222	0.1128	-0.0517
5	-0.2028	0.2427	-0.0747	-0.2288	0.0715	-0.0404	-0.0630	0.0907	0.1808	0.0450
6	0.2690	0.1549	-0.2111	0.1097	0.1759	-0.0402	-0.1472	-0.1527	-0.0824	-0.0462
7	0.3852	-0.0189	-0.1233	-0.0500	0.0733	-0.0763	-0.0982	0.1026	0.0797	-0.0464
8	0.4261	-0.1134	-0.1852	-0.0843	-0.0713	0.0280	-0.0111	0.1184	0.1541	-0.2268
9	0.3810	-0.1505	-0.0466	-0.1050	-0.1349	0.0136	0.1012	0.0840	0.1805	-0.1696
10	0.3752	-0.1493	-0.1041	-0.1373	-0.1852	-0.0119	0.0308	0.0941	0.0794	-0.0614
11	0.3357	-0.1644	-0.3611	-0.0961	-0.1132	0.2021	0.0891	0.1224	0.0465	-0.2126
12	0.3706	-0.0706	-0.4592	-0.0628	-0.1203	0.1963	0.0517	0.0576	0.0576	-0.1817
13	0.1549	-0.2269	-0.2671	-0.1206	-0.1019	0.2921	-0.1687	0.0123	0.0493	-0.1951
14	0.2587	0.0509	-0.2807	0.0315	0.0034	0.0518	-0.1090	-0.1218	0.0380	-0.2631
15	0.4007	-0.0790	-0.4129	-0.0029	-0.0538	0.0820	0.0536	0.0004	0.0568	-0.1414
16	0.3127	-0.0516	-0.2546	-0.0550	0.0951	0.0691	-0.0134	-0.0278	-0.0410	-0.0779
17	0.2544	-0.0844	-0.4346	-0.0422	0.1369	0.0463	0.0370	0.0274	-0.0176	-0.0142
18	-0.0935	-0.2099	-0.0868	-0.1056	-0.0119	0.2701	-0.3116	0.0118	-0.1113	-0.0971
19	0.0602	0.1602	-0.1517	0.1293	0.1209	-0.0035	-0.0836	-0.2073	-0.0197	-0.1904
20	0.3957	-0.1626	-0.3076	-0.1108	-0.0557	0.1116	0.1189	0.1152	0.2118	-0.1863
21	0.1926	0.1004	-0.1066	0.1070	0.1358	-0.1264	-0.1272	-0.1813	-0.0287	-0.0962
22	0.2857	-0.1733	0.0677	-0.0711	-0.2173	-0.0422	0.0597	-0.0178	0.1522	-0.2207
23	0.4600	-0.1552	-0.0873	-0.0511	-0.1231	-0.0772	0.0452	0.0850	0.2485	-0.2707
24	0.4107	-0.1256	-0.0839	0.0725	0.0449	-0.1242	-0.0180	0.0138	0.1634	-0.1798
25	0.4088	-0.0506	-0.1204	0.1320	0.1005	-0.1859	-0.0888	-0.0624	0.1036	-0.1690
26	0.2117	0.2439	-0.1020	0.0881	0.2037	-0.0927	-0.2044	-0.0986	0.0452	-0.1435
27	0.2619	0.2671	-0.1165	0.1416	0.2587	-0.1536	-0.2529	-0.1008	-0.0236	-0.0345
28	0.4780	-0.1623	-0.0726	-0.0751	-0.1871	-0.1008	0.0531	0.1142	0.1648	-0.0828
29	0.1540	0.2751	-0.1008	0.2462	0.2247	-0.1565	-0.1624	-0.2074	-0.0655	-0.0586
30	0.2568	0.1907	-0.1193	0.2796	0.2086	-0.2137	-0.2381	-0.1575	-0.0566	-0.0279
31	0.1704	0.1161	-0.0411	0.1362	-0.0141	-0.1812	-0.1741	-0.1584	-0.0417	-0.0982
32	0.2905	-0.1637	0.1067	-0.0914	-0.4832	-0.3663	-0.0659	-0.1264	-0.1447	-0.1332
33	0.0515	-0.0627	0.1536	-0.0369	-0.2102	0.0230	0.0503	-0.1452	-0.0821	-0.0098
34	0.2965	-0.1599	0.2603	-0.0886	-0.4550	-0.3862	-0.0779	-0.0833	-0.1388	0.1527
35	0.4075	-0.1757	0.2117	-0.0720	-0.3605	-0.3459	-0.0760	-0.0307	-0.0352	0.0747
36	0.3130	-0.1808	0.3056	-0.0974	-0.4473	-0.3757	-0.0499	-0.0839	-0.1308	0.1626
37	0.3438	-0.1774	0.1853	-0.1079	-0.4708	-0.3868	-0.1030	-0.0286	-0.0670	0.1186
38	0.4223	-0.1127	0.0116	-0.1059	-0.3313	-0.2406	-0.0456	0.0360	0.0284	0.0402
39	0.3820	0.0450	0.0479	0.0163	-0.0163	-0.2970	-0.2237	0.0392	0.0608	0.0461
40	0.2800	-0.1228	0.2949	-0.0852	-0.4562	-0.3256	-0.0173	-0.1183	-0.1720	0.1798
41	-0.1404	0.2265	-0.0073	0.1154	-0.0016	-0.0961	0.1295	-0.2009	-0.0598	-0.0790
42	-0.1627	0.2482	-0.0131	0.3979	-0.0149	-0.0988	0.1247	-0.2088	-0.0578	-0.1470
43	-0.2054	0.1686	0.0029	0.3931	-0.0736	-0.0881	0.1589	-0.1663	-0.0293	-0.1542
44	-0.1234	0.0951	0.0905	0.1022	-0.0995	0.0761	0.0817	-0.0777	-0.0156	-0.0775
45	-0.3266	-0.1155	0.0141	0.5265	-0.1251	-0.0976	0.1728	0.0437	0.1224	-0.0800
46	-0.3498	0.0042	-0.0908	0.4643	-0.0447	-0.1788	0.0482	0.0968	0.0437	-0.0259
47	-0.2630	0.0730	-0.1211	0.2957	-0.0230	-0.1764	0.0720	-0.0185	-0.0502	-0.0331
48	-0.1558	0.1726	-0.0740	0.3503	0.0075	-0.1571	0.0820	-0.2027	-0.0482	-0.1326
49	-0.2563	-0.0548	-0.1201	0.4577	-0.0440	-0.1815	0.1058	-0.0459	-0.0207	-0.0428
50	-0.3012	-0.2637	-0.1340	0.1038	0.0053	-0.0451	-0.1287	0.0877	0.0073	0.0107
51	0.1586	0.1179	-0.2847	0.2221	0.0994	0.0014	0.0827	-0.1089	-0.2538	0.2545
52	0.1381	-0.0039	-0.2619	0.1033	0.0112	0.0122	0.0906	0.0226	-0.0843	0.1817
53	-0.0221	-0.0821	-0.2815	-0.0607	0.1037	0.0578	-0.1580	0.1181	-0.1857	0.0936
54	0.0108	0.1876	-0.1908	0.2474	0.1017	-0.1458	-0.0539	-0.1040	-0.1653	0.0631
55	0.0327	0.0915	-0.3541	0.2197	0.0473	0.0437	0.1904	-0.0790	-0.2490	0.2889
56	0.3050	-0.0180	-0.3606	-0.1078	-0.1971	0.1976	0.1834	0.1576	0.0019	0.0887
57	0.2838	-0.0121	-0.3755	-0.1459	-0.1864	0.1739	0.2042	0.1801	0.0527	0.1202
58	0.2253	0.1358	-0.3925	-0.0425	-0.0776	0.1253	0.1233	0.0440	-0.0695	0.1098
59	0.2688	0.0049	-0.3939	-0.1409	-0.2484	0.1896	0.2026	0.1507	0.0550	0.0264
60	0.3218	0.0232	-0.3538	-0.0119	-0.0784	0.1181	0.1326	0.0998	-0.0712	0.2112
61	-0.1108	0.3819	0.0402	0.0634	0.0042	-0.0515	-0.0047	-0.1830	-0.0328	-0.1866
62	-0.1941	0.4248	0.1298	-0.0729	-0.1017	0.0629	0.0325	-0.0236	0.0358	-0.1581
63	-0.1307	0.2196	0.1188	0.1279	-0.0853	0.0745	0.0396	-0.0484	-0.0064	-0.0747
64	-0.0829	0.1884	0.0681	0.0673	-0.0272	0.0499	-0.0197	-0.1409	-0.0155	-0.1071
65	-0.1272	0.1602	0.0584	0.0526	-0.0525	-0.0327	-0.0166	-0.1387	0.0389	-0.2163
66	-0.2087	0.5401	0.1775	-0.1255	-0.1353	0.0903	-0.0505	0.1992	0.1217	-0.0812
67	-0.0350	0.3895	0.1352	-0.0757	0.0678	-0.0373	-0.2284	0.2504	0.0743	0.1181
68	-0.1531	0.4741	0.0821	-0.1168	-0.0515	0.0302	-0.1320	0.1637	0.0662	-0.0555
69	-0.1185	0.5112	0.2048	-0.0966	-0.0872	0.0989	-0.1155	0.1999	0.0687	-0.0139
70	-0.1544	0.4774	0.1700	-0.0992	-0.0587	0.0881	-0.1434	0.2565	0.0636	0.0219
71	-0.1780	0.4462	0.1590	-0.0421	-0.1492	0.0965	0.0140	0.0397	0.0349	-0.1371
72	-0.0163	0.3766	0.1578	-0.1320	0.0515	-0.0074	-0.2647	0.2589	0.0290	0.1047
73	-0.1814	0.5444	0.1738	-0.1494	-0.1140	0.0880	-0.0750	0.1918	0.0789	-0.0380
74	-0.1289	0.5960	0.1396	-0.1594	-0.0449	0.0553	-0.1174	0.2550	0.1028	0.1032
75	-0.2064	0.4837	0.1797	-0.0639	-0.1650	0.1199	0.0497	0.1288	0.0662	-0.0479
76	-0.2126	0.4493	0.1277	-0.0688	-0.1872	0.0885	0.1978	-0.0107	-0.0716	0.0200
77	-0.2380	0.3022	0.1097	-0.2200	-0.1896	0.0592	0.1425	0.1099	-0.0831	0.1353
78	-0.2011	0.3331	0.1282	-0.0927	-0.1732	0.0943	0.1586	0.0579	-0.0256	0.0754
79	-0.2335	0.4459	0.1515	-0.1214	-0.1871	0.0964	0.1331	0.0743	0.0366	-0.0279
80	-0.1887	0.2447	0.1202	-0.1736	-0.1858	0.0365	0.0857	0.1221	-0.1042	0.1497
81	0.4264	-0.1679	0.2297	-0.0191	0.1743	-0.0762	-0.0207	0.1854	0.0949	-0.0349
82	0.3137	-0.2217	0.3691	-0.0154	0.2888	0.0694	0.1131	0.1440	0.0800	-0.0318
83	0.3627	-0.1563	0.3426	0.0414	0.3947	0.0211	0.0829	0.1900	0.1675	0.0467
84	0.4397	-0.1602	0.3663	-0.0020	0.3110	-0.0258	0.0707	0.2140	0.1257	0.1124
85	0.3500	-0.1259	0.4013	0.0536	0.3663	0.0186	0.0698	0.2221	0.1352	0.1052
86	0.1489	-0.0428	0.2863	0.0629	0.2783	0.1643	0.1091	0.0431	-0.0279	0.0630
87	0.2536	-0.0928	0.3238	0.0118	0.0170	-0.1176	-0.0480	0.0419	-0.0776	0.2076
88	0.2551	-0.1764	0.4585	0.0349	0.2330	0.1627	0.2377	0.0260	-0.0370	-0.0769
89	0.2558	-0.1397	0.4260	0.0652	0.3421	0.1688	0.1771	0.1013	-0.0044	0.0292
90	0.1983	-0.1693	0.4695	0.0416	0.2758	0.2508	0.2899	0.0264	-0.0399	-0.1075
91	0.0822	-0.0808	0.1908	0.0313	0.1276	0.1724	0.0898	-0.0560	-0.0325	-0.0647
92	0.1387	-0.1704	0.4591	0.0076	0.1368	0.2771	0.3243	-0.0812	-0.1434	-0.1772
93	0.0357	-0.1135	0.2827	-0.0121	-0.0541	0.2228	0.2184	-0.1867	-0.1762	-0.1768
94	0.0825	-0.1575	0.4196	-0.0071	0.0085	0.2714	0.3095	-0.1839	-0.2319	-0.1972
95	0.1025	-0.1768	0.3908	-0.0218	-0.0297	0.2711	0.2959	-0.1764	-0.2260	-0.2253
96	0.2197	0.0661	0.0338	0.1303	0.2937	-0.0902	-0.2525	0.0517	-0.1642	0.1751
97	0.5086	-0.0448	0.2322	0.1086	0.3762	-0.0335	-0.0855	0.1085	-0.0237	0.1859
98	0.2571	0.1401	0.0879	0.1912	0.3298	-0.1108	-0.2376	0.0184	-0.1013	0.2474
99	0.2885	0.0265	0.1424	0.1365	0.3859	0.0061	-0.1170	0.0652	-0.0162	0.1263
100	0.2439	0.0881	0.1671	0.1351	0.2223	-0.1270	-0.2198	0.0523	-0.0878	0.2861
101	0.0955	-0.1428	0.2364	-0.0269	-0.2455	-0.0498	0.0161	-0.1809	-0.0332	-0.0124
102	-0.2160	-0.2166	-0.0119	-0.0892	-0.0416	0.1075	-0.2184	-0.0427	0.0527	0.0132
103	-0.2170	-0.2002	0.0380	0.0218	-0.0438	0.2509	-0.2297	-0.2382	0.3033	0.2303
104	-0.1420	-0.1927	0.1128	-0.0042	-0.1085	0.4196	-0.3184	-0.4722	0.3103	0.2649
105	-0.1312	-0.1879	0.1058	0.0140	-0.1235	0.4160	-0.3095	-0.4940	0.3357	0.2578
106	-0.3407	-0.2455	-0.0540	0.0962	0.0616	-0.0343	-0.0369	0.1198	0.3184	0.2135
107	-0.4309	-0.1459	0.0093	0.4758	-0.1475	-0.1026	0.1803	0.1740	0.2021	-0.0228
108	-0.3921	-0.1961	0.0197	0.5108	-0.1607	-0.0845	0.1693	0.1534	0.1931	-0.0470
109	-0.4070	-0.1296	-0.0040	0.3786	-0.1169	-0.1130	0.2035	0.1309	0.2121	-0.0083
110	-0.4339	-0.2379	-0.0413	0.2437	-0.0653	-0.0616	0.0667	0.1547	0.2558	0.1006
111	0.1194	0.1198	-0.2981	-0.0459	0.0237	0.1931	0.2636	0.0200	-0.1797	0.3358
112	0.0830	-0.0086	-0.2672	-0.0930	-0.0042	0.1848	0.2947	0.0224	-0.1180	0.3320
113	-0.0779	0.1401	-0.1830	-0.0241	0.0483	0.0850	0.2651	-0.1582	-0.1899	0.3066
114	0.0113	0.1697	-0.2211	0.0924	0.0163	0.1343	0.2511	-0.1592	-0.2621	0.2814
115	0.0327	0.0470	-0.2768	-0.1166	0.1379	0.1326	0.2192	0.0139	-0.1060	0.3986
116	-0.4769	-0.3140	-0.0731	0.1744	0.0249	-0.1232	0.1123	0.1323	0.2650	0.1568
117	-0.2148	-0.3407	-0.0923	-0.0565	0.1503	-0.2248	0.1555	0.0118	0.2509	0.1171
118	-0.4536	-0.3466	-0.0665	-0.0261	0.0852	-0.1155	0.0721	0.0269	0.2768	0.1578
119	-0.4218	-0.1953	-0.0604	-0.2459	0.1873	-0.2705	0.2222	-0.1423	0.1176	0.0211
120	-0.4772	-0.3068	-0.0993	-0.1891	0.1768	-0.2530	0.1989	-0.1025	0.1840	0.0809
121	-0.0600	-0.0724	0.1102	0.0050	-0.0876	0.2367	-0.1016	-0.2586	0.0538	0.0446
122	-0.2875	-0.1869	0.0464	-0.0846	-0.1282	0.0612	-0.1088	0.1703	-0.2764	0.0614
123	-0.3415	-0.1401	0.0270	-0.0446	-0.1667	-0.0145	-0.0583	0.1939	-0.2464	0.0592
124	-0.1074	-0.1604	0.1065	-0.0184	-0.1331	0.4062	-0.2827	-0.4077	0.1930	0.1383
125	-0.1992	-0.2282	0.0990	-0.0150	-0.1518	0.4000	-0.3809	-0.3960	0.1163	0.1263
126	-0.4678	-0.4397	-0.1171	0.0744	0.0263	0.0502	-0.1961	0.2742	-0.1212	0.0136
127	-0.4074	-0.4061	-0.0346	0.2253	-0.0764	0.1255	-0.2882	0.3257	-0.3021	-0.1665
128	-0.3236	-0.3699	-0.0314	0.1861	-0.0832	0.2186	-0.3651	0.2628	-0.3539	-0.1774
129	-0.3160	-0.3144	-0.0255	0.1248	-0.0540	0.1540	-0.3034	0.2628	-0.4255	-0.2137
130	-0.3501	-0.3317	-0.0142	0.1360	-0.0851	0.2196	-0.3673	0.3159	-0.3211	-0.1632
131	-0.3716	0.0238	-0.0555	-0.3627	0.1521	-0.2029	0.0379	0.0092	0.0740	-0.0111
132	-0.4006	-0.1083	-0.0666	-0.4100	0.1686	-0.1761	-0.0186	-0.0344	-0.0004	-0.0091
133	-0.3151	-0.1821	-0.0585	-0.4268	0.1569	-0.1491	-0.0155	-0.0310	-0.0396	-0.0666
134	-0.1925	0.1469	0.0914	-0.0415	-0.0575	-0.0023	0.1570	-0.1493	0.0071	-0.1138
135	-0.3188	0.0891	0.0281	-0.1370	0.0280	-0.1143	0.1972	-0.0901	0.0629	-0.0536
136	-0.3796	-0.1831	-0.0671	-0.4412	0.1755	-0.2000	0.0432	-0.1380	-0.2154	-0.1597
137	-0.2843	-0.1603	-0.0602	-0.4325	0.2133	-0.1681	0.0072	-0.1977	-0.1511	-0.1305
138	-0.3015	-0.2007	-0.0559	-0.4460	0.2256	-0.1456	0.0118	-0.1642	-0.1648	-0.1252
139	-0.3783	-0.0944	-0.0781	-0.4100	0.2296	-0.2481	0.1024	-0.1484	-0.1248	-0.1228
140	-0.4466	-0.1781	-0.1071	-0.4327	0.2301	-0.2171	0.0411	-0.0499	-0.1124	-0.0775

KEY TO SAMPLES IN APPENDIX 5

SAMPLE No's	SITE
1-20	6
21-40	10
41-60	8
61-80	11
81-100	2
101-120	3
121-140	4

In all cases the origin of the samples within a site were in the following order:

time I, A to E;

time II, A to E;

time III, A to E;

time IV, A to E.

Thus sample number 21 is 10 I A, sample 22 is 10 I B and sample number 36 is 10 IV A etc..

REFERENCES

ABRAMS P. (1977) Density-independent mortality and interspecific competition: A test of Painka's niche overlap hypothesis. *Am. Nat.* 111: 539-552

ALBRIGHT L.J. (1976) *In situ* degradation of mangrove tissues. *N.Z. J. Mar. Freshwat. Res.* 10: 385-389

ALLER R.C. and YINGST J.Y. (1978) Biogeochemistry of tube dwellings: A study of the sedentary polychaete *Amphitrite ornata* (Leidy). *J. Mar. Res.* 36: 201-54

ALONGI D.M. and TIETJEN J.H. (1980) Population growth and trophic interactions among free-living marine nematodes. In: *Marine Benthic Dynamics*, (K.R. Tenore & B.C. Coull, eds), pp 151-166. Univ. Sth Carolina Press: Columbus, SC.

AMJAD S. and GRAY J.S. (1983) Use of the nematode-copepod ratio as an index of organic pollution. *Mar. Poll. Bull.* 14: 178-181

ANDERSON G.I.R.V., EHRLICH A.H., EHRLICH P.R., ROUGHGARDEN J.D., RUSSELL B.C. and TALBOT F.H. (1981) Community structure of coral reef fishes. *Am. Nat.* 117: 476-495

ANDREWARTHA H.C. and BIRCH L.C. (1954) *The Distribution of Animals.* University of Chicago Press: Chicago.

AUCLAIR A.N. and GOFF F.G. (1971) Diversity relations of upland forests in the western Great Lakes area. *Am. Nat.* 105: 499-528

BAILLIE P.W. and WELSH B.L. (1980) The effect of tidal resuspension on the distribution of intertidal epipelic algae in an estuary. *Est. Coast. Mar. Sci.* 10: 165-180

BELL S.S. (1979) Short and long-term variation in a high marsh meiofauna community. *Est. Coast. Mar. Sci.* 9: 331-350

BELL S.S. (1980) Meiofauna-macrofauna interactions in a high salt marsh habitat. *Ecol. Monogr.* 50: 487-505

BELL S.S. and COULL B.C. (1978) Field evidence that shrimp predation regulates meiofauna. *Oecologia* 35: 141-148

BELL S.S., WATZIN M.C. and COULL B.C. (1978) Biogeneic structure and its effect on the spatial heterogeneity of meiofauna in a salt marsh.
*J. exp. Mar. Biol. Ecol.*35: 99-107

BILIO M. (1967) Nahrungsbeziehungen der turbellarien in Kustensalzweisen.
Helgolander wiss. Meeresunters. 15: 602-621

BLOOM S.A. (1981) Similarity indices in community studies: Potential pitfalls.
Mar. Ecol. Preg. Ser. 5: 125-128

BOADEN P.J.S. (1964) Grazing in the interstitial habitat: A review.
Brit. Ecol. Soc. Symp. 4: 299-303

BOADEN P.J.S. (1968) Water movement - a dominant factor in interstitial ecology.
Sarsia 34: 125-136

BOADEN P.J.S. (1977) Thiobiotic facts and fancies (aspects of the distribution and evolution of anaerobic meiofauna). In: *The Meiofauna Species in Time and Space*, (W. Sterrer & P. Ax, eds), pp 45-63. Midrofauna Meeresboden, 61.

BOADEN P.J.S. and PLATT H.M. (1971) Daily migration patterns in an intertidal - meiobenthic community.
Thallassia. Jugosl. 7: 1-12

BOESCH D.F., WASS M.L. and VIRNSTEIN R. (1976) The dynamics of estuarine benthic communities. In: *Estuarine Processes* Vol. 1, (M.L. Wiley, ed.), pp 177-96. Academic Press: London

BOUCHER G. (1973) Premieres donnees ecologiques sur les nematodes libres marins d'une station de vas Cotiere de Banyuls.
Vie Milieu. 23(B): 69-100

BOUCHER G. (1980) Impact of 'Amoco cadiz' oil spill on intertidal and sublittoral meiofauna.
Mar. Pollut. Bull. 11: 95-101

BOUCHER G. and CHAMROUX S. (1976) Bacteria and meiofauna in an experimental sand ecosystem. I. Material and preliminary results.
J. exp. Mar. Biol. Ecol. 24: 237-249

BRAY J.R. and CURTIS J.T. (1957) An ordination of the upland forest communities of southern Wisconsin.
Ecol. Monogr. 27: 325-349

BROWN J.H. and LIEBERMAN G.A. (1973) Resource utilisation and co-existence of seed eating desert rodents in sand dune habitats.
Ecology 54: 788-797

BUCHANAN J.B., KINGSTON P.F., SHEADER M. (1974) Long-term population trends of the benthic macrofauna in the offshore mud of the Northumberland coast.
J. Mar. Biol. Ass. UK. 54: 785-795

BUSS L.W. and JACKSON J.B.C. (1979) Competitive networks: nontransitive competitive relationships in cryptic coral reef environments.
Am. Nat. 113: 223-234

CAIN R.L. and DEAN J.M. (1975) Annual occurrence, abundance and diversity of fish in a south Carolina intertidal creek.
Mar. Biol. 36: 369-379

CAIRNS J., PLAFKIN J.L., KAESLER R.L. and LOWE R.L. (1983) Early colonisation patterns of diatoms and protozoa in 14 freshwater lakes.
J. Protozool. 30: 47-51

CAPSTICK C.K. (1959) The distribution of free living nematodes in relation to salinity in the middle and upper reaches of the River Blyth estuary.
J. Anim. Ecol. 28: 189-210

CHAMROUX S., BOUCHER G. and BODIN P. (1979) Etude experimentale d'un ecosysteme sableux. II. Evolution des populations de bacteries et de meiofaune.
Helgolander wiss. Meeresunters. 30: 163-177

CHANDLER G.T. and FLEEGER J.W. (1983) Meiofaunal colonisation of Azoic estuarine sediment in Louisiana: Mechanisms of dispersal.
J. exp. Mar. Biol. Ecol. 69: 175-188

CHESSON P.L. and WARNER R.R. (1981) Environmental variability promotes existence in lottery competitive systems.
Am. Nat. 117: 923-943

CLARKE L.D. and HANNON N.J. (1967) The mangrove swamp and salt marsh communities of the Sydney district. I. Vegetation, soils and climate.
J. Ecol. 55: 753-771

CLARKE L.D. and HANNON N.J. (1969) The mangrove swamp and salt marsh communities of the Sydney district. II. The holocoenotic complex with particular reference to physiography.
J. Ecol. 57: 213-234

CLARKE L.D. and HANNON N.J. (1970) The mangrove swamp and salt marsh communites of the Sydney district. III. Plant growth in relation to salinity and water logging.
J. Ecol. 58: 351-369

CLARKE L.D. and HANNON N.J. (1971) The mangrove swamp and salt marsh communites of the Sydney district. IV. The significance of species interaction.
J. Ecol. 59: 535-553

CODY M.L. (1968) On the methods of resource division in grassland bird communities.
Am. Nat. 102: 107-148

CONNELL J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*.
Ecology 42: 710-723

CONNELL J.H. (1970) A predator-prey system in the marine intertidal region. I. *Balanus Glandula* and several predatory species of *Thais*.
Ecol. Monogr. 40: 49-78

CONNELL J.H. (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: *Ecology & Evolution of Communities*, (M.L. Cody & J.M. Diamond, eds), pp 460-512. Belknap P.: Cambridge, Mass.

CONNELL J.H. (1978) Diversity in tropical rainforests and coral reefs.
Science 199: 1302-1310

CONNOR E.F. and SIMBERLOFF D. (1979) The assembly of species communities: Chance or competition.
Ecology 60: 1132-1140

COULL B.C. (1969) Hydrographic control of meiofauna in Bermuda.
Limnol. Oceanogr. 14: 953-957

COULL B.C. (1973) Estuarine meiofauna: A review. Trophic relations and microbial interactions. In: *Estuarine Microbial Ecology*, (L.H. Stevenson & R.R. Colwell, eds), pp 499-512. Univ. Sth Carolina Press: Columbus, S.C.

COULL B.C. and FLEEGER J.W. (1977) Long-term temporal variation and community dynamics of meiobenthic copepods.
Ecology 58: 1136-1143

COULL B.C. and WELLS J.B.J. (1981) Density of mud-dwelling meiobenthos from three sites in the Wellington region.
N.Z. J. Mar. Freshwat. Res. 15: 411-415

COULL B.C., HICKS G.R.F. and WELLS J.B.J. (1981) Nematode/copepod ratios for monitoring pollution: A rebuttal. *Mar. Poll. Bull.* 12: 378-381

CULVER D. (1970) Analysis of simple cave communities: Niche separation and species packing. *Ecology* 51: 949-958

CUNDELL A.M., BROWN M.S., STANFORD R. and MITCHELL R. (1979) Microbial degradation of *Rhizophora mangle* leaves immersed in the sea. *Est. Coast Mar. Sci.* 9: 281-286

DAUER D.M. and SIMON J.L. (1976) Habitat expansion among polychaetous anneldids repopulating a defaunated marine habitat. *Mar. Biol.* 37: 169-177

DAVIS N. and VAN BLARICOM G. (1978) Spatial and temporal heterogeneity in a sand bottom epifaunal community of invertebrates in shallow water. *Limnol. Oceanogr.* 23: 417-427

DAY R.W. (1977) Two contrasting effects of predation on species richness in coral reef habitats. *Mar. Biol.* 44: 1-5

DAYTON P.K. (1971) Competition, distrubance and community organisation: the provision and subsequent utilisation of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389

DAYTON P.K. (1973) Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. *Am. Nat.* 107: 662-670

DEUTCH A. (1978) Gut structure and digestive physology of two marine nematodes, *Chromadorina germanica* (Butchili 1847) and *Diplolaimella* sp. *Biol. Bull.* 155: 317-335

DIAMOND J.M. (1975) Assembly of species communities. In: *Ecology and Evolution of Communities*, (M.L. Cody and J.M. Diamond, eds), pp 342-444. Belknap Press: Cambridge, Mass.

DICKSON K.L. and CAIRNS J.Jr. (1972) The relationship of freshwater macroinvertebrate communities collected by artificial floating substrates to the Macarthur-Wilson equilibrium model. *Am. Midl. Nat.* 88: 68-75

DUGAN P.J. and LIVINGSTON R.J. (1982) Long-term variation of macro-invertebrate assemblages in Apalachee Bay, Florida. *Est. Coast. Shelf Sci.* 14: 391-403

DYER K.R. (1981) Localised mixing of low salinity patches in a partially mixed estuary (Southampton Water, England). In: *Estuarine Comparisons*, (V.S. Kennedy, ed.), pp 21-36. Academic Press: London.

EAGLE R.A. (1975) Natural fluctuations in a soft bottom benthic community.
J. Mar. Biol. Ass. UK. 55: 865-878

EAGLE R.A. and HARDIMAN P.A. (1977) Some observations on the relative abundance of species in a benthic community. In: *Biology of Benthic Organisms: 11th European Symposium on Marine Biology*, (B.F. Keegan, P.D. Ceidigh & P.J.S. Boaden, eds), pp 197-208. Pergamon Press: Oxford.

ECKMAN J.E. (1979) Small-scale patterns and processes in a soft-substratum, intertidal community.
J. Mar. Res. 37: 437-457

FAGER E.W. (1971) Pattern in the development of a marine community.
Limnol. Oceanogr. 16: 241-253

FAUCHAULD K. and JUMARS P.A. (1979) The diet of worms: A study of polychaete feeding guilds.
Ann. Rev. Mar. Biol. Oceanogr. 17: 193-294

FEHON W.C. and OLIVER J.D. (1979) Taxonomy and distribution of surface microlayer bacteria from two estuarine sites.
Estuaries 2: 194-197

FENCHEL T. (1970) Studies on the decomposition of organic detritus derived from turtle grass *Thalassia testudinum*.
Limnol. Oceanogr. 15: 14-20

FENCHEL T.M. and KOLDING S. (1979) Habitat selection and distribution patterns of five species of the amphipod genus *Gammarus*.
Oikos 33: 316-322

FENCHEL T.M. and REIDL R.J. (1970) The sulphide system: a new biotic community underneath the oxidised layer of marine sand bottoms.
Mar. Biol. 7: 255-268

FERRIS V.R., FERRIS J.M., BERNARD R.L. and PROBST A.H. (1971) Community structure of plant parasitic nematodes related to soil types in Illinois and Indiana soybean fields.
J. Nematol. 3: 399-408

FINDLAY S.E.G. (1981) Small scale spatial distribution of meiofauna on a mud- and sandflat.
Est. Coast. Shelf. Sci. 12: 471-484

FINDLAY S.E.G. (1982) Effect of detrital nutritional quality on population dynamics of a marine nematode (*Diplolaimelloides chitwoodi*).
Mar. Biol. 68: 223-227

FISHER R.A. and YATES F. (1957) *Statistical Tables for Biological, Agricultural and Medical Research*. (5th Ed.). Oliver and Boyd, Edinburgh.

FLEEGER J.W. (1980) Community structure of an estuarine meiobenthic copepod assemblage.
Est. Coast. Mar. Sci. 10: 107-118

FLEEGER J.W., WHIPPLE S.A. and COOK L.L. (1982) Field manipulations of tidal flushing, light exposure and natant macrofauna in a Louisiana salt marsh: Effects on the meiofauna.
J. exp. Mar. Biol. Ecol. 46: 87-100

GALLOWAY R.W. (1982) Distribution and physiographic patterns of Australian mangroves. In: *Mangrove Ecosystems in Australia*, (B.F. Clough, ed.), pp 31-54. ANU Press: Canberra.

GARDENER W.S. and HANSEN R.B. (1979) Dissolved free amino acids in interstitial waters of Georgia salt marsh soils.
Estuaries 2: 113-118

GAUCH H.G. Jr. (1982) *Multivariate Analysis in Community Ecology*. Cambridge University Press: Cambridge.

GERLACH S.A. (1953) Die biozonotische gliderung der ematoden beseidlung an der Deutchen kusten.
Z. Morph. Okol. Tiere. 41: 411-512

GERLACH S.A. (1971) On the importance of meiofauna for benthos communities.
Oecologia 6: 176-190

GERLACH S.A. (1977a) Means of meiofauna dispersal. In: *The Meiofauna Species in Time and Space*, (W. Sterrer & P. Ax, eds), pp 89-103. Mikrofauna Meeresboden, 61.

GERLACH S.A. (1977b) Attraction to decaying organisms as a possible cause for patchy distribution of nematodes in a Bermuda beach.
Ophelia 16: 151-165

GERLACH S.A. (1978) Food chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity.
Oecologia 33: 55-69

GERLACH S.A. and SCHRAGE M. (1969) Freilebende nematoden als nahrung der sandgarnele *Grangon grangon*. Experimentelle untersuchungen uber die bedeutung der meiofauna als nahrung fur das marine makrobenthos.
Oecologia 2: 362-375

GERLACH S.A. and SCHRAGE M. (1971) Life cycles in marine meiobenthos. Experiments at various temperatures with *Monhystera disjuncta* and *Theristus pertenuis* (Nematoda).
Mar. Biol. 9: 274-280

GIERE O. (1979) The impact of oil pollution on intertidal meiofauna. Field studies after the Lacoruna-spill, May 1976.
Cah. Biol. Mar. 20: 231-251

GLASSER J.W. (1979) The role of predation in shaping and maintaining the structure of communities.
Am. Nat. 113: 631-641

GLEMAREC M. and MENESGUEN A. (1980) Functioning of a muddy sand ecosystem: Seasonal fluctuations of different trophic levels and difficulties in estimating production of the dominant macrofauna species. In: *Marine Benthic Dynamics*, (K.R. Tenore & B.C. Coull, eds), pp 49-68. Univ. Sth Carolina Press: Columbus S.C.

GLYN P.W. (1976) Some physical and biological determinants of coral community structure in the eastern pacific.
Ecol. Monogr. 46: 431-456

GOULTER P.F.E. and ALLAWAY W.G. (1979) Litter fall and decomposition in a mangrove stand, *Avicennia marina* (Forsk.) Verh. in Middle Harbour, Sydney.
Aust. J. Mar. Freshw. Res. 30: 541-546

GOWER J.C. (1966) Some distance properties of latent root and vector methods in multivariate analysis.
Biometrika 53: 325-338

GRAY J.S. (1971) The effects of pollution on sand meiofauna communities.
Thallass. Jugosl. 7: 79-86

GRAY J.S. (1981) Detecting pollution induced changes in communities using the log-normal distribution of individuals among species.
Mar. Poll. Bull. 12: 173-176

GREEN R.H. (1966) Measurement of non-randomness in spatial distributions.
Res. Pop. Ecol. 8: 1-7

GROSSMAN G.D. (1982) Dynamics and organization of a rocky intertidal fish assemblage: Persistence and resilience of taxocene structure.
Am. Nat. 119: 611-637

GRUBB P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche.
Biol. Rev. 52: 107-145

HAGERMAN G.M. and RIEGER R.M. (1981) Dispersal of benthic meiofauna by wave and current action in Bogue Sound, North Carolina, USA.
Mar. Ecol. 2: 245-271

HARPER J.L. (1969) The role of predation in vegetational diversity.
Brookhaven Symp. Biol. 22: 48-62

HEBERT P.D.N. (1974a) Enzyme variations in natural populations of *Daphnia magna*. II. Genotypic frequencies in permanent populations.
Genetics. 77: 324-333

HEBERT P.D.N. (1974b) Enzyme variability in natural population of *Daphnia magna*. III. Genotypic frequencies in intermittent populations.
Genetics 77: 335-341

HEIP C. and DECRAEMER W. (1974) The diversity of nematode communities in the southern North Sea.
J. Mar. Biol. Ass. UK. 54: 251-255

HEIP C. and SMOL N. (1976) On the importance of *Protohydra leuckarti* as a predator of meiobenthic populations.
Proceedings 10th European Marine Biology Ostend. 2: 285-296

HEIP C., SMOL N. and ABSILLIS V. (1978) Influence of temperature on the reproductive potential of *Oncholaimus oxyuris* (Nematoda: Oncholaimidae).
Mar. Biol. 45: 255-260

HOCKIN D.C. and OLLASON J.G. (1981) The colonisation of artificially isolated volumes of intertidal estuarine sand by harpacticoid copepods.
J. exp. Mar. Biol. Ecol. 53: 9-29

HODDA M. and NICHOLAS W.L. (1985) The meiofauna associated with mangroves in the Hunter River and Fullerton Cove.
Aust. J. Mar. Freshwat. Res. 36: 41-50

HOGUE E.W. and MILLER C.B. (1981) Effects of sediment microtopography on small-scale spatial distribution of meiobenthic nematodes.
J. exp. Mar. Biol. Ecol. 53: 181-191

HOPPER B.E. and MEYERS S.P. (1966) Observations on the bionomics of the marine nematode *Metoncholaimus* sp.
Nature 209: 899-900

HOPPER B.E. and MEYERS S.P. (1967a) Population studies on benthic nematodes within a subtropical seagrass community.
Mar. Biol. 1: 85-96

HOPPER B.E. and MEYERS S.P. (1967b) Folicolous marine nematodes on turtle grass, *Thalassia testudinum* Konig, in Biscayne Bay, Florida.
Bull. Mar. Sci. 17: 471-517

HOPPER B.E., FELL J.W. and CEFALU R.C. (1973) Effect of temperature on life cycles of nematodes associated with the mangrove (*Rhizophora mangle*) detrital system.
Mar. Biol. 23: 293-296

HORN H.S. and MACARTHUR R.H. (1972) Competition among fugitive species in a harlequin environment.
Ecology 53: 749-752

HOTELLING H. (1933) Analysis of a complex of statistical variables into principal components.
J. Educ. Psych. 24: 417-441, 498-520.

HOWELL R. (1983) Heavy metals in marine nematodes: Uptake, tissue distribution and loss of copper and zinc.
Mar. Poll. Bull. 14: 263-268

HUSTON M. (1979) A general hypothesis of species diversity.
Am. Nat. 113: 81-101

HYLLEBERG J. (1975) Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms.
Ophelia 14: 113-117

JACKSON J.B.C. (1972) The ecology of molluscs of *Thalassia* communities, Jamaica, West Indies. II. Molluscan population variability along an environmental stress gradient.
Mar. Biol. 14: 304-337

JACKSON J.B.C. (1977) Habitat area, colonisation and development of epidbenthic community structure. In: *Biology of Benthic Organisms* (B.F. Keegan, P. O. Ciedigh and P.J.S. Boaden, eds), pp 349-358. Pergamon Press: London.

JACKSON J.B.C. and WINSTON J.E. (1982) Ecology of cryptic coral reef communities. I. Distribution and abundance of major groups of encrusting organisms.
J. exp. Mar. Biol. Ecol. 54: 135-147

JAEGER R.G. (1971) Competitive exclusion as a factor influencing the distribution of two species of terrestrial salamanders. *Ecology* 52: 632-637

JANSSON B.O. (1967) The availability of oxygen for the interstitial fauna of sandy beaches. *J. exp. Mar. Biol. Ecol.* 1: 123-143

JANZEN D.H. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 501-528

JENSEN P. (1981) Phyto-chemical sensitivity and swimming behaviour of the free-living marine nematode *Chromadorita tenuis*. *Mar. Ecol. Prog. Ser.* 4: 203-206

JOHNSON S.R., FERRIS J.M. and FERRIS V.R. (1973) Nematode community structure in forest woodlots. II. Ordination of nematode communities. *J. Nematol.* 5: 95-107

JOHNSON S.R., FERRIS J.M. and FERRIS V.R. (1974) Nematode community structure in forest woodlots. III. Ordinations of Taxonomic groups and biomass. *J. Nematol.* 6: 118-126

JOHNSON S.R., FERRIS V.R. and FERRIS J.M. (1972) Nematode community structure of forest woodlots. I. Relationships based on similarity coefficients of nematode species. *J. Nematol.* 4: 175-183

JUARIO J.V. (1975) Nematode species composition and seasonal fluctuations of a sublittoral meiofauna community in the German Bight. *Veroff. Inst. Meeresforsch. Bremerh.* 15: 283-337

KAESLER R.L. and CAIRNS J.Jr (1969) Cluster analysis of Potomac River survey stations based on protozoan presence-absence data. *Hydrobiologia* 34: 414-432

KAESLER R.L. and CAIRNS J.Jr (1972) Cluster analysis of data from limnological surveys of the upper Potomac River. *Am. Midl. Nat.* 88: 56-67

KARR J.R. (1971) Structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr.* 41: 207-233

KASTENDIEK J. (1982) Competitor mediated coexistence: interactions among three species of benthic macroalgae. *J. exp. Mar. Biol. Ecol.* 62: 201-210

KEMP W.M., WETZEL R.L., BOYNTON W.R., DIELIA C. and STEVENSON J.C. (1981) Nitrogen cycling and estuarine interfaces: some current concepts and research directions. In: *Estuarine Comparisons*, (V.S. Kennedy, ed), pp 209-230. Academic Press: London

KENT B.W. (1983) Patterns of coexistence in busyconine whelks. *J. exp. Mar. Biol. Ecol.* 66: 257-283

KEOUGH M.J. (1983) Patterns of recruitment of sessile invertebrates in two sub-tidal habitats. *J. exp. Mar. Biol. Ecol.* 66: 213-245

KNEIB R.T. (1982) Habitat preference, predation and the intertidal distribution of gammaridean amphipods in a North Carolina salt marsh. *J. exp. Mar. Biol. Ecol.* 59: 219-230

KOHN A.J. (1959) The ecology of *Conus* in Hawaii. *Ecol. Monogr.* 29: 47-90

KOHN A.J. (1968) Microhabitats, abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. *Ecology* 49: 1046-1061

KOHN A.J. (1971) Diversity, utilisation of resources and adaptive radiation in shallow water marine invertebrates of tropical oceanic islands. *Limnol. Oceanogr.* 16: 332-348

KOOP K., NEWELL R.C. and LUCAS M.I. (1981) Biodegradation and carbon flow based on kelp debris (*Ecklonia maxima*) in a sandy beach microcosm. *Mar. Ecol. Prog. Ser.* 7: 315-326

LAMONT B.B. and GRANT K.J. (1979) A comparison of twenty-one measures of site dissimilarity. In: *Multivariate Methods in Ecological Work*, (L. Orloci, C.R. Rao & W.M. Stiteler, eds), pp 101-126. International Cooperative Publishing: Fairland, Maryland, USA.

LANCE G.N. and WILLIAMS W.T. (1967a) A general theory of classificatory sorting strategies. *Computer J.* 10: 271-277

LANCE G.N. and WILLIAMS W.T. (1967b) Mixed data classificatory programs. I. Divisive systems. *Aust. Computer J.* 1: 82-85

LANG J. (1973) Interspecific aggression by scleratinian corals. II. Why race is not only to the swift. *Bull. Mar. Sci.* 23: 260-279

LASSERE P., RENAUD-MORNANT J. and CASTEL J. (1976) Metabolic activities of meiofauna communities in a semi-enclosed lagoon. Possibilities of trophic competition between meiofauna and mugilid fish.
Proc. 10th Eur. Mar. Biol. Symp. 12: 393-414

LEE J.J., TIETJEN J.H., MASTROPAOLO C. and RUBIN H. (1977) Food quality and the heterogeneous spatial distribution of meiofauna.
Helgolander wiss. Meeresunters 30: 272-282

LEGENDRE L. and LEGENDRE P. (1983) *Numerical Ecology*. Elsevier Scientific Publ. Co.: Oxford.

LEVIN S.A. (1974) Dispersion and population interactions.
Am. Nat. 108: 207-228

LEVIN S.A. and PAINE R.T. (1974) Disturbance, patch formation and community structure.
Proc. Nat. Acad. Sci. USA 71: 2744-2747

LEVINS R. and CULVER D. (1971) Regional coexistence of species and competition between rare species.
Proc. Nat. Acad. Sci. USA 68: 1246-1248

LEVINTON J.S. and STEWART S. (1982) Marine succession: the effect of two deposit-feeding gastropod species on the population growth of *Paranais litoralis* Muller 1784 (Oligochaeta).
J. exp. Mar. Biol. Ecol. 59: 231-241

LEWIS M.R. and PLATT T.W. (1981) Scales of variability in estuarine ecosystems. In: *Estuarine Comparisons*, (V.S. Kennedy, ed.), pp 3-20. Academic Press: London

LEWONTIN R.C. (1969) The meaning of stability.
Brookhaven Symp. Biol. 22: 13-34

LOTKA A.J. (1932) The growth of mixed populations: Two species competing for a common food supply.
J. Wash. Acad. Sci. 22: 461-469

LOUCKS O.L. (1970) Evolution of diversity, efficiency and community stability.
Am. Zool. 10: 17-25

LOYA Y. (1976) Recolonisation of red sea corals affected by natural catastrophes and man-made perturbations.
Ecology 57: 278-289

LUBCHENCO J. (1980) Algal zonation in the New England rocky intertidal community: an experimental analysis.
Ecology 61: 333-344

LUBCHENKO J. and MENGE B.A. (1978) Community development and persistence in a low rocky intertidal zone.
Ecol. Monogr. 48: 67-94

MAGUIRE C. (1977) Meiofaunal community structure and vertical distribution: A comparison of some Co. down beaches. In: *Biology of Benthic Organisms: 11th European Symposium on Marine Biology*, (B.F. Keegan, P.D. Geidigh & P.J.S. Boaden, eds), pp 197-208. Pergamon Press: Oxford.

MARCOTT B.M. and COULL B.C. (1974) Pollution, diversity and meiobenthic communities in the North Adriatic (Bay of Piran, Yugoslavia).
Vie Milieu 24: 281-300

MENGE B.A. (1976) Organisation of the New England rocky intertidal community: role of predation, competition and temporal heterogeneity.
Ecol. Monogr. 46: 355-369

MEYERS S.P. and HOPPER B.E. (1973) Nematological-microbial interrelationships and estuarine biodegrative processes. In: *Estuarine Microbial Ecology*, (L.H. Stevenson & R.R. Colwell, eds), pp 483-489. Univ. Sth. Carolina Press: Columbus S.C

MEYERS S.P., HOPPER B.E. and CEFALU R. (1970) Ecological investigations of the marine nematode *Metoncholaimus scissus*.
Mar. Biol. 6: 43-47

MOLL R.A. and ROHLF F.J. (1981) Analysis of temporal and spatial phytoplankton variability in a Long Island salt marsh.
J. exp. Mar. Biol. Ecol. 51: 133-144

MONTAGNA P.A. and RUBER E. (1980) Decomposition of *Spartina alternifolia* in different seasons and habitats of a northern Massachusetts salt marsh and comparison with other Atlantic regions.
Estuaries 3: 61-63

MOTYKA J., DOBRZANSKI B. and ZAWADZKI S. (1950) Wstepne badania nad lakami puludniowo wschodniej Lubelszczyzny. Ann. Univ. Mariae Curie Sklowowska Sect. E.: Agricultura 5: 367-447 [quoted in Legendre and Legendre (1983)]

McINTYRE A.D. (1964) Meiobenthos of sub-littoral muds.
J. Mar. Biol. Ass. UK. 44: 665-674

McINTYRE A.D. (1968) The meiofauna and microfauna of some tropical beaches.
J. Zool. 156: 377-392

McINTYRE A.D. (1969) Ecology of marine meiobenthos.
Biol. Rev. 44: 245-290

McINTYRE A.D. and MURISON D.J. (1973) The meiofauna of a flatfish nursery ground.
J. Mar. Biol. Ass. UK. 53: 93-118

McLACHLAN A. (1978) A quantitative analysis of the meiofauna and the chemistry of the redox potential discontinuity zone in a sheltered sandy beach.
Est. Coast Mar. Sci. 7: 275-290

McLACHLAN A., WINTER P.E.D. and BOTHA L. (1977) Vertical and horizontal distribution of sub-littoral meiofauna in Algoa Bay, South Africa.
Mar. Biol. 40: 355-364

NICHOLAS W.L. (1984) *Biology of Free-living Nematodes.* Clarendon Press: Oxford.

NICHOLSON A.J. (1933) The balance of animal populations.
J. Anim. Ecol. 2: 132-178

NICHOLSON A.J. (1954) An outline of the dynamics of animal populations
Aust. J. Zool. 2: 9-65

ODUM W.E. (1970) Utilisation of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus*. In: *Marine Food Chains*, (J.H. Steele, ed.), pp 222-240. Oliver and Boyd: Edinburgh.

ODUM W.E. and HEALD E.J. (1972) Trophic analysis of an estuarine mangrove community.
Bull. Mar. Sci. 22: 671-738

ODUM W.E. and HEALD E.J. (1975) The detritus based food web of an estuarine mangrove community. In: *Estuarine Research* Vol.1 (L.E. Cronin, ed.), pp 265-286. Academic Press: New York.

ORIANS G.H. and HORN H.S. (1969) Overlap in foods of four species of blackbirds in the potholes of Central Washington.
Ecology 50: 930-938

ORLOCI L. (1979) Non-linear data structures and their description. In: *Multivariate Methods in Ecological Work*, (L. Orloci, C.R. Rao & W.M. Stiteler, eds), pp 191-202. International Cooperative Publishing: Fairland, Maryland, USA.

OSENGA G.A. and COULL B.C. (1983) *Spartina alternifolia* Loisel root structure and meiofaunal abundance.
J. exp. Mar. Biol. Ecol. 67: 221-225

OSMAN R.W. (1977) The establishment and development of a marine epifaunal community.
Ecol. Monogr. 47: 37-63

OTT J. and SCHIEMER F. (1973) Respiration and anaerobiosis of free living nematodes from marine and limnic sediments.
Neth. J. Sea Res. 7: 233-243

PAINE R.T. (1966) Food web complexity and species diversity.
Am. Nat. 100: 65-75

PAINE R.T. (1971) A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat.
Ecology 52: 1096-1106

PATRICK R. (1967) The effect of invasion rate species pool and size of area on the structure of the diatom community.
Proc. Nat. Acad. Sci. US 58: 1335-1345

PATRICK W.H. Jr., and DeLAUNE R.D. (1977) Chemical and biological redox systems affecting nutrient availability in the coastal wetlands.
Geoscience & Man 18: 131-137

PERKINS E.J. (1958) The food relationships of the microbenthos, with particular reference to that found at Whitstable, Kent.
Ann. Mag. Nat. hist. Ser. 131: 64-77

PETERSON C.H. (1975) Stability of species and community for the benthos of two lagoons.
Ecology 56: 958-965

PIANKA E.R. (1965) On lizard species diversity: North American flatland deserts.
Ecology 48: 333-351

PIANKA E.R. (1969) Sympatry of desert lizards (*Ctenotus*) in Western Australia.
Ecology 50: 1012-1030

PIANKA E.R. (1971) Lizard species density in the Kalahari desert.
Ecology 52: 1024-1029

PIANKA E.R. (1976) Competition and niche theory. In: *Theoretical Ecology, Principles and Applications*, (R.M. May, ed.), pp 114-141. Saunders: Philadelphia.

PIELOU E.P. (1975) *Ecology Diversity.* Wiley-Interscience: Sydney.

PLATT H.M. (1981) Meiofaunal dynamics and the origin of the metazoa. In: *The Evolving Biosphere* (P.L. Forey, ed.), pp 207-216. British Museum (Natural History): London.

PLATT H.M. and WARWICK R.M. (1980) The significance of free-living nematodes to the littoral ecosystem. In: *The Shore Environment Vol. 2 Ecosystems*, (J.H. Price, D.E.G. Irvine & W.F. Farnham, eds), pp 729-759. Academic Press: London.

PORTER J. (1972a) Predation by *Acanthaster* and its effect on coral species diversity.
Am. Nat. 106: 487-492

PORTER J. (1972b) Patterns of species diversity in Caribbean reef corals.
Ecology 53: 745-748

PORTER J. (1974) Community structure of coral reefs on opposite sides of the Isthmus of Panama.
Science 186: 543-545

PRESTON F.W. (1962) The canonical distribution of commonness and rarity.
Ecology 43: 185-215, 410-432

PRICE R. and WARWICK R.M. (1980) The effect of temperature on the respiration rate of meiofauna.
Oecologia 44: 145-148

PULLIAM H.R. (1975) Coexistence of sparrows: a test of community theory.
Science 189: 474-476

RAFFAELLI D.G. (1981) Monitoring with meiofauna: a reply to Coull, Hicks & Wells (1981) and additional data.
Mar. Poll. Bull. 12: 381-382

RAFFAELLI D.G. and MASON C.F. (1981) Pollution monitoring with meiofauna, using the ratio of nematodes to copepods
Mar. Poll. Bull. 12: 158-163

RAINER S. (1981) Temporal patterns in the structure of macrobenthic communities of an Australian estuary.
Est. Coast Shelf Sci. 13: 597-620

READ P.A., ANDERSON K.J., MATTHEWS J.E., WATSON P.A., HALLIDAY M.C. and SHEILS G.M. (1983) Effects of pollution on the benthos of the Firth or Forth.
Mar. Poll. Bull. 14: 12-16

REES C.B. (1940) A preliminary study of the ecology of a mudflat.
J. Mar. Biol. Ass. UK. 24: 185-199

REISE K. (1979) Moderate predation on meiofauna by the macrobenthos of the Wadden Sea.
Helgolander wiss. Meenesunters. 32: 453-465

REISE K. (1983) Experimental removal of lugworms from marine sand affects small zoobenthos.
Mar. Biol. 74: 327-332

REVELANTE N., WILLIAMS W.T. and BUNT J.S. (1982) Temporal and spatal distribution of diatoms, dinoflagellates and *Trichodesmium* in waters of the Great Barrier Reef.
J. exp. Mar. Biol. Ecol. 63: 27-45

REX M. (1977) Zonation in deep sea gastropods: the importance of biological interactions to rates of zonation. In: *Biology of Benthic Organisms: 11th European Symposium on Marine Biology*, (B.F. Keegan, P.D. Ceidigh & P.J.S. Boaden, eds), pp. 521-530. Pergamon Press: Oxford.

RIEGER R. and OTT J. (1971) Gezietenbedigte Wanderungen von Turbellarien und nematoden eines nordadriaischen sandstrandes.
Vie et rev Suppl, 22: 425-447

ROUGHGARDEN J.D. (1974) Species packing and the competition function with illustrations from coral reef fish.
Theor. Pop. Biol. 5: 163-186

ROUGHGARDEN J.D. and FELDMAN M. (1975) Species packing and predation pressure.
Ecology 56: 489-492

RUBLEE P.A. (1981) Bacteria and microbial distribution in estuarine sediments. In: *Estuarine Comparisons*, (V.S. Kennedy, ed.), pp 159-182. Academic Press: London.

RUTZLER K. and STERRER W. (1970) Oil pollution: damage observed in tropical communities along the Atlantic seaboard of Panama.
BioScience 20: 222-224

SALE P.F. (1975) Patterns of use of space in a guild of territorial reef fishes.
Mar. Biol. 29: 89-97

SALE P.F. (1977) Maintainence of high diversity in coral reef communities.
Am. Nat. 111: 337-359

SALE P.F. (1979) Recruitment, loss and co-existence in a guild of territorial coral reef fishes.
Oecologia 42: 159-177

SALE P.F. (1980) Assemblages of fish on patch reefs - predictable or unpredictable.
Environ. Biol. Fishes 5: 243-249

SALE P.F. and DYBDAHL R. (1975) Determinants of community structure for Coral Reef fishes in an experimental habitat. *Ecology* 56: 1343-1355

SANDERS H.L. (1968) Marine benthic diversity: a comparative study. *Am. Nat.* 102: 243-282

SCHOENER T.W. (1968) The *Anolis* Lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704-726

SCHOENER T.W. (1974a) Resource partitioning in ecological communities. *Science* 185: 27-39

SCHOENER T.W. (1974b) Competition and the form of habitat shift. *Theor. Pop. Biol.* 6: 265-307

SHAW K.M., LAMBSHEAD P.J.D. and PLATT H.M. (1983) Detection of pollution induced disturbance in marine benthic assemblages with special reference to nematodes. *Mar. Ecol. Prog. Ser.* 11: 195-202

SHERMAN K.M. and COULL B.C. (1980) The response of meiofauna to sediment disturbance. *J. exp. Mar. Biol. Ecol.* 45: 59-71

SIBERT J.R. (1981) Intertidal hyperbenthic populations in the Nanaimo estuary. *Mar. Biol.* 46: 259-265

SIKORA W.B. and SIKORA J.P. (1982) Ecological implications of the vertical distribution of meiofauna in salt marsh sediments. In: *Estuarine Comparions*, (V.S. Kennedy ed.), pp 269-282. Academic Press: London

SLATKIN M. (1974) Competition and regional coexistence. *Ecology* 55: 121-134

SNEATH P.H.A. and SOKAL R.R. (1973) *Numerical Taxonomy: the Principles and Practice of Numerical Classification.* W.H. Freeman & Co.: San Francisco.

SOUSA W.P. (1979a) Disturbance in marine intertidal boulder fields: the non-equilibrium maintainence of species diversity. *Ecology* 60: 1225-1239

SOUSA W.P. (1979b) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.* 49: 227-254

STERRER W. (1973) Plate tectonics as a mechanism for dispersal and speciation in interstitial sand fauna.
Neth. J. Sea Res. 7: 200-222

SUREY-GENT S.C. (1981) Distribution of *Anoplostoma viviparum* (Nematoda) in Southampton water sediments.
Mar. Biol. 62: 157-160

SUTHERLAND J.P. and KARLSON R.H. (1977) Development and stability of the fouling community at Beaufort, North Carolina.
Ecol. Monogr. 47: 425-446

SWEDMARK B. (1964) The interstitial fauna of marine sand.
Biol. Rev. 39: 1-42

TALBOT F.H., RUSSELL B.C. and ANDERSON G.R.V. (1978) Coral reef fish communities: unstable, high-diversity systems.
Ecol. Monogr. 48: 425-440

TAYLOR P.R. (1982) Environmental resistance and the ecology of coexisting hermit crabs: thermal tolerance.
J. exp. Mar. Biol. Ecol. 57: 229-236

TEAL J.M. and WIESER W. (1966) The distribution and ecology of nematodes in a Georgia salt marsh.
Limnol. Oceanogr. 11: 217-222

TERBORGH J. (1971) Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru.
Ecology 52: 23-40

THORNE G. (1961) *Principles of Nematology.* McGraw-Hill: London

THORSON G. (1966) Some factors influencing the recruitment and establishment of marine benthic communities.
Neth. J. Sea. Res. 3: 267-293

TIETJEN J.H. (1969) The ecology of shallow water meiofauna in two New England estuaries.
Oecologia 2: 251-291

TIETJEN J.H. (1976) Distribution and species diversity of deep-sea nematodes off North Carolina.
Deep Sea Research 23: 255-278

TIETJEN J.H. (1977) Population distribution and structure of the free-living nematodes of Long Island Sound.
Mar. Biol. 43: 123-136

TIETJEN J.H. (1980) Population structure and species composition of the free-living nematodes inhabiting sands of the New York Bight apex.
Est. Coast. Mar. Sci. 10: 61-73

TIETJEN J.H. and LEE J.J. (1972) Life cycles of marine nematodes. Influence of temperature and salinity on the development of *Monhystera denticulata* Timm.
Oecologia 10: 167-176

TIETJEN J.H. and LEE J.J. (1977a) Life histories of marine nematodes. Influences of temperature and salinity on the reproductive potential of *Chromadorina germanica* Butschli. In: *The Meiofauna Species in Time and Space* (W. Sterrer & P. Ax eds), pp 263-270. Mikrofauna Meeresboden, 61.

TIETJEN J.H. and LEE J.J. (1977b) Feeding behaviour of marine nematodes. In: *Ecology of Marine Benthos*, (B.C. Coull ed.), pp 21-35. Univ. of South Carolina Press: Columbus S.C.

TIETJEN J.H., LEE J.J., RULLMAN J., GREENGART A. and TROMPETER J. (1970) Gnotobiotic culture and physiological ecology of the marine nematode *Rhabditis marina* Bastian.
Limnol. Oceanogr. 15: 535-543

UBBEN M.S. and HANSON R.B. (1980) Tidal induced regulation of nitrogen fixation activity (C_2H_4) production in a Georgia salt marsh.
Est. Coast Mar. Sci. 10: 445-453

VANCE R.R. (1972) Competition and mechanism of coexistence in three sympatric species of hermit crabs.
Ecology 53: 1062-1074

VIDAKOVIC J. (1983) The influence of raw domestic sewage on density and distribution of meiofauna.
Mar. Poll. Bull. 14: 84-88

VINCE S.J., VALIELA N., BACKUS N. and TEAL J.M. (1976) Predation by the salt marsh killfish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance.
J. exp. Mar. Biol. Ecol. 23: 255-266

VIRNSTEIN R.W. (1977) The importance of predation by crabs and fishes on infauna in Chesapeake Bay.
Ecology 58: 1199-1217

VITELLO P. (1970) Marine nematodes associations in the muddy bottoms of provence. I. Muddy sediments in sheltered areas and terrigenous coastal muds (English summary).
Ann. Inst. Oceanogr. Paris 50: 145-172

VOLTERRA V. (1976) Variatzione E fluctuazione Del numero D'individui in specie animali conviventi.
Mem. R. Acad. Lincei. Ser. 6, II.

Van BLARICOM G.R. (1982) Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell.
Ecol. Monogr. 52: 283-305

Van DOLAH R.F. (1978) Factors regulating the distribution and population dynamics of the amphipod *Gammarus palustris* in an intertidal salt marsh community.
Ecol. Monogr. 48: 191-217

Van ES F.B., Van ARKEL M.A., BOUWMAN L.A. and SCHRODER H.G.J. (1980) Influence of organic pollution on bacterial, macrobenthic and meiobenthic populations in intertidal flats of the Dollard.
Neth. J. Sea Res. 14: 288-304

WARD A.R. (1973) Studies on the sublittoral free-living nematodes of Liverpool Bay. I. The structure and distribution of the nematode populations.
Mar. Biol. 22: 53-66

WARD A.R. (1975) Studies on the sublittoral free-living nematodes of Liverpool Bay. II. Influence of sediment composition on the distribution of marine nematodes.
Mar. Biol. 30: 217-225

WARWICK R.M. (1971) Nematode associations in the Exe estuaries.
J. Mar. Biol. Ass. UK 51: 439-454

WARWICK R.M. (1977) The structure and seasonal fluctuations of phytal marine nematode association on the Isles of Scilly. In:
Biology of Benthic Organisms: 11th European Symposium on Marine Biology, (B.F. Keegan, P.D. Ceidigh & P.J.S. Boaden eds), pp 577-586. Pergamon Press: Oxford.

WARWICK R.M. (1981a) Influence of temperature and salinity on energy partitioning in the marine nematode *Diplolaimelloides brucei*.
Oecologia 51: 318-325

WARWICK R.M. (1981b) The nematode/copepod ratio and its use in pollution ecology.
Mar. Poll. Bull. 12: 329-333

WARWICK R.M. and BUCHANAN J.B. (1970) The meiofauna off the coast of Northumberland. I. The structure of the nematode population. *J. Mar. Biol. Ass. UK* 50: 129-146

WARWICK R.M. and BUCHANAN J.B. (1971) The meiofauna off the coast of Northumberland. II. Seasonal stability of the nematode population. *J. Mar. Biol. Ass. UK* 51: 355-362

WARWICK R.M. and PRICE R.W. (1975) Macrofauna production in an estuarine mud flat. *J. Mar. Biol. Ass. UK.* 55: 1-18

WARWICK R.M. and PRICE R.W. (1979) Ecological and metabolic studies on free-living nematodes from an estuarine mud flat. *Est. Coast Mar. Sci.* 9: 257-271

WHITTAKER R.H. (1952) A study of summer insect communities in the Great Smoky Mountains. *Ecol. Monogr.* 22: 1-44

WIENS J.A. (1977) On competition and variable environments. *Am. Sci.* 65: 592-597

WIESER W. (1953) Die beziehung zwischen mundohohlengestalt, ernahrungsweise und vorkommen bei freilenbenden marinen nematoden. *Ark. Zool.* 4: 439-484

WIESER W. (1959) Free-living marine nematodes. IV. General part. *Acta Univ. Lund. N.F.* Adv. 2, 50: 1-148

WIESER W. (1960) Benthic studies in Buzzards Bay. II. The meiofauna. *Limnol. Oceanogr.* 5: 121-137

WIESER W. and KANWISHER J.W. (1961) Ecological and physiological studies on marine nematodes from a small salt marsh near Woods Hole, Massachusetts. *Limnol. Oceanogr.* 6: 262-270

WIESER W. and SCHIEMER F. (1977) The ecophysiology of some marine nematodes from Bermuda: seasonal aspects. *J. exp. Mar. Biol. Ecol.* 26: 97-106

WIESER W., OTT J., SCHIEMER F. and GNAIGER E. (1974) An ecophysiological study of some meiofauna species inhabiting a sandy beach at Bermuda. *Mar. Biol.* 26: 235-248

WILLEMS K.A., VINCX M., CLAEYS D., VANOSMAEL C. and HEIP C. (1982) Meiobenthos of a sublittoral sandbank in the southern bight of the North Sea.
J. Mar. Biol. Ass. UK 62: 535-548

WILLIAMS W.T., CLAY H.J. and BUNT J.S (1982) The analysis, in marine ecology, of three-dimensional data matrices with one dimension of variable length.
J. exp. Mar. Biol. Ecol. 60: 189-196

WILLIAMS W.T., LAMBERT J.M. and LANCE G.N. (1968) Multivariate methods in plant ecology. V. Similarity indices and information analysis.
J. Ecol. 54: 427-445

WOODIN S.A. (1974) Polychaete abundance patterns in a soft-sediment environment: the importance of biological interactions.
Ecol. Monogr. 44: 171-187

WOODIN S.A. (1978) Refuges, disturbance and community structure: a marine soft-bottom example.
Ecology 59: 274-284

WOODROFFE C.D. (1981) Litter production and decomposition in the New Zealand mangrove, *Avicennia marina* var. *resinifera*.
N.Z. J. Mar. Freshwat. Res. 16: 179-188

WORMALD A.P. (1976) Effects of a spill of marine diesel oil on the meiofauna of a sandy beach at Picnic Bay, Hong Kong.
Environ. Pollut. 11: 117-130

WORMALD A.P. and STIRLING H.P. (1979) A preliminary investigation of nutrient enrichment in experimental sand columns and its effect on tropical intertidal bacteria and meiofauna.
Est. Coast Mar. Sci. 8: 441-453

YINGST J.Y. (1978) Patterns of micro- and meiofaunal abundance in marine sediments, measured with the adenosine triphosphate assay.
Mar. Biol. 47: 41-54

YODZIS P. (1981) The structure of assembled communities.
J. theor. Bio. 92: 103-118

ZARET T.M. and RAND A.S. (1971) Competition in tropical stream fishes: support for the competitive exclusion principle.
Ecology 52: 236-342